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THE DEVELOPMENT OF THE VASCULAR STRUCTURE OF DIANTHERA AMERICANA (WITH PLATES I-IV). *W. Ralph Jones* - - -

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THE DEVELOPMENT OF THE VASCULAR STRUCTURE OF DIANTHERA AMERICANA

W. RALPH JONES

(WITH PLATES I–IV)

In 1907, THEO. HOLM (5), in describing the anatomical structure of *Dianthera americana*, called attention to the "polystelic" condition of the stem. This paper seems to be the only one ever published on this intensely interesting plant. So at the suggestion of Professor DUNCAN S. JOHNSON, I have made a study of the ontogenetic development of the stelar structure in order to find out how the "polystelic" condition of the mature plant is derived.

The material studied consisted of seedlings grown in the laboratory and greenhouse from seeds collected near the Chain Bridge (over the Potomac River about four and one-half miles above Washington, D.C.), of seedlings collected at the Chain Bridge, and of mature plants from Chain Bridge and from near Betterton, Md.

Most of the material studied was imbedded in paraffin, and sectioned 5–10 μ thick. Various stains were used, but the best results were obtained with methyl green and acid fuchsin.

Dianthera americana is a perennial herb, with an erect stem 3–9 dm. high, grooved and angled, usually simple, and having opposite, simple, linear-lanceolate leaves 75–150 mm. long and 6–15 mm. wide. At the Chain Bridge, the plant grows in the tide pools on the rocky flats on the north side of the river, and also along the banks of the Chesapeake and Ohio Canal, which at this point runs parallel to the river just back of the flats. The plant produces flowers from May on through the summer, ripening its fruits from

about the middle of July to the end of summer. The fruit, a loculicidal two-celled capsule, dehisces violently, often throwing the four seeds a distance of several decimeters. The seeds germinate very soon after being shed, the seedlings reaching a height of about 2 dm. by the end of the growing season. Branches formed in the axils of the basal leaves, and at first growing upward, soon curve, and grow downward to just below the surface of the water, then take a nearly horizontal direction. These stolons, becoming 0.5–1 dm. long, send out adventitious roots at the nodes that pass downward into the mud.

At the end of the growing season, the vertical shoot dies down to just below the usual level of the water, usually to the top of the first node below the surface. The rest of the stem remains green and apparently in good condition for some time, but gradually rotting. The stolons, with their scalelike leaves, where exposed to the light, remain green throughout the winter, as do also the upper parts of the adventitious roots. In the spring, the terminal bud of the stolon again starts its activity, turning upward, and sending up a vertical shoot into the air. This shoot develops elongated leaves, and rarely branches from near the base. The basal buds, however, usually produce the rhizomes by means of which the plant perennates. Buds formed in the axils of the upper leaves develop into the capitate-spicate inflorescences of violet or nearly white flowers.

At Betterton, Md., the plant grows under different conditions. Instead of growing in the water, it grows in the sand just above the level of high tide; the rhizomes grow about on the level of the top of the moist sand, the lower one to three internodes of the aerial shoot being buried in dry sand. The basal branches grow upward a few centimeters, turn down, and then become horizontal, growing along the top of the moist sand at a depth of 5–10 cm. below the surface. The basal part of the erect shoots and also the rhizomes, therefore, are without chlorophyll. Although many discharged capsules were seen, I could find no trace of seedlings, so I cannot say that the life-history here is the same as at Chain Bridge, but from the time of flowering and of the ripening of the seeds, and from the general habit of the plants, I see no reason for believing that there are any marked differences in the general life-history.

As HOLM (5) has pointed out, both the vertical aerial stem and the horizontal submerged rhizome show, in a cross-section of an internode, six peripheral and one central bundle, each of leptome, hadrome, and pith, and each completely surrounded by a thin-walled endodermis, each having, therefore, the appearance of a complete stele (fig. 8). For this reason, HOLM says that the plant is polystelic; from its development, however, it will be seen that it is really astelic.

At each node there is a fusion of the six peripheral meristeles to form a complete ring of vascular tissue, which breaks up in a very regular way to form the six peripheral meristeles of the internode above (fig. 1). Each of the bundles of the lower internode divides at the node to form a Y; then each branch fuses with a branch of the adjacent Y, thus giving rise to the six peripheral bundles of the next internode. The single leaf traces join the vascular system of the stem at the crotches of two opposite Y's. The two bundles which supply the traces are usually, though not always, larger than the other four. There is also a connection made, at each node, between the central bundle and the peripheral ring of vascular tissue by means of a transverse arm, coming out from the central bundle at right angles to it and fusing with the vascular ring just below the insertion of the leaf traces (figs. 3–8 show a series of transverse sections through the node). The structure of the node next above or next below the one described is exactly the same, except that its plane of symmetry is at right angles to that of the adjacent one, as is shown in fig. 1. A diagram of the path of the bundles in a mature plant is shown in fig. 2.

The seeds

The seeds (figs. 11 and 12) are much flattened, and are nearly circular in outline. They are about 2–3 mm. in diameter, and about 0.75–1 mm. in thickness. On the lower side the edge of the seed is slightly hollowed out to form a pocket in which lie the hilum and the micropyle. The testa is brown in color, and has a much roughened surface, owing to the distortion of the underlying cells, of which there are two to four layers (fig. 10). The walls of the epidermal cells are thickened in bands which fuse at some places, and at others taper to a point and disappear. The inner

cells are thin-walled, and are much distorted in shape. The endosperm is represented by a thin pellicle, usually two cells in thickness, except at the lower edge of the seed, where it thickens to form a mass of appreciable thickness, which forms a cap over the free end of the hypocotyl. The well developed embryo nearly fills the seed. The two large cotyledons are flat, nearly circular in outline, accumbent, the curved hypocotyl lying closely against the edges of the cotyledons, and being free only at the end. The seed, therefore, corresponds very closely to that of *Dianthera nodosa* Benth. & Hook. as described by SCHAFFNIT (**8,** p. 65).

The epidermis of the hypocotyl is composed of small cells which are elongated vertically. The cortex consists of about ten layers of cells, radially arranged, and of larger diameter than those of the epidermis. They are flattened vertically, and appear nearly square in cross-section. The innermost layer appears in no way different from the rest of the cortex. One striking feature of this layer, however, is the division of its cells, on each side of the central cylinder between the protoxylem poles, to form two layers (fig. 14). Schizogenous air cavities, of small diameter, but of considerable length, have already formed between the angles of the adjoining cells.

The central cylinder is sharply marked off from the surrounding cortex, owing to its greatly elongated cells of very small diameter (fig. 14). Just below the insertion of the cotyledons, the central cylinder divides to form the two procambial cotyledonary traces (fig. 13).

Germination

The earliest stages of germination have not been observed in the field. Seeds brought into the laboratory and soaked in water swelled about 0.5 mm. in diameter and about 0.25 mm. in thickness. These soaked seeds were then placed in a moist chamber, either on wet filter paper or on wet sand. The testa soon split, the hypocotyl pushing through. Further growth now forces upward the upper end of the hypocotyl and the cotyledons, often carrying the testa still clinging to one or both of the cotyledons. The latter soon become green, continue their growth, and function photosynthetically for some time. The plumule is rather tardy in starting its growth.

For ease of description, we will divide the growth of the seedling into stages corresponding to the number of pairs of leaves present.

STAGE I

The first seedling stage (fig. 15) shows the elongating hypocotyl well out of the testa, pushing upward the cotyledons which are frequently still inclosed within the testa. All the endosperm found in the seed has been used up. The primordia of the first pair of leaves are beginning to develop, but no sign of differentiation of the foliar traces has yet appeared. From each cotyledon one double bundle enters the hypocotyl (fig. 16). These bundles approach each other, and very soon come together to form the central cylinder.

In the middle of the hypocotyl, a cross-section shows an epidermis of cells slightly elongated radially, the inner and side walls thin, the outer walls slightly cutinized; the cortex, about 10–12 cells in thickness, the outer two or three layers of irregularly arranged cells, which are beginning to show a slight thickening and later forming a typical collenchyma. The remaining inner layers of the cortex are made up of rounded thin-walled cells, very regularly arranged in radial rows, their walls being in contact except at the angles, where there are formed small schizogenous air cavities, which latter extend vertically for a considerable distance. The innermost layer of the cortex is not modified in any way, being like the other cells of the inner part of the cortex in size, shape, and content of cells.

The central cylinder, or stele, is very sharply marked off from the surrounding cortex, being made up of much smaller cells except at the very center. The pericycle is of one layer except opposite the xylem poles, where it is of two layers. The xylem is arranged in two opposite groups, the protoxylem being exarch. The four phloem groups are placed one on each side of the xylem poles. The rest of the central cylinder is of thin-walled parenchyma, small near the periphery, but becoming much larger at the center. There are no air spaces in the central cylinder.

Transition.—In the petiole of each of the cotyledons is a double bundle, the protoxylem of which occupies an endarch position. As the two bundles of the cotyledons enter the hypocotyl, there is

a rotation of the xylem, the protoxylem becoming exarch. On reaching the transition region, near the base of the hypocotyl, the phloem of each bundle divides, and passes to the right and left of the xylem. Each half moves to the side of the stele, finally fusing with a half of the phloem from the other bundle. This forms a typical diarch root, the transition being that of Type III of VAN TIEGHEM. Fig. 17 shows a diagram of the path of the vascular tissue at this stage.

STAGE II

In the second stage, the first pair of leaves have enlarged sufficiently to be seen easily by the naked eye (fig. 19). The primordia of the second pair of leaves are not differentiated until near the end of this stage. The bases of the cotyledons have fused to form a short tube. The leaves of the first pair are opposite and are decussate to the cotyledons. As they develop, there begins the differentiation of a single vascular bundle for each, the differentiation beginning at the node, passing outward into the leaf, and downward into the stem, passing through the very short epicotyl into the hypocotyl, and becoming inserted between the cotyledonary bundles, the protoxylems finally disappearing near the base of the hypocotyl.

There have also started to develop two buds, one axillary to each cotyledon, but at this stage neither shows any differentiation of vascular tissue. A diagram of the course of the vascular tissue at this stage is shown in fig. 18.

The cortex and epidermis are very nearly as in the preceding stage, the angles of the outer cortical cells being more thickened, however, and the outer wall of the epidermal cells being heavier than before. Glandular hairs of the type found on the mature plant (figs. 26 and 27) are numerous on the hypocotyl and cotyledons.

At the close of this period of development, a bundle develops on each side of the stem between the two traces of the first pair of leaves. These bundles, at the lower end, are forked just over the cotyledonary traces, the forks being inserted on either side of the traces, between them and the bundles from the first leaves. At the upper end, the bundles fork, the branches passing off nearly

at right angles to the main bundle, and being inserted on the sides of the leaf traces of the first pair of leaves. There is thus formed a complete ring of vascular tissue in the first epicotylar node. Rarely the forks at the base of the bundles are of very unequal size, or one of the bundles may even fail to divide, in this case merely bending aside, and becoming inserted on one side or the other of one of the cotyledonary traces. The direction of differentiation of these side bundles seems to be acropetal, but this could not be made out definitely. The cross-arms connecting the bundles with the traces of the first pair of leaves, however, are undoubtedly younger than the main part of the bundles. Fig. 20 shows the course of the bundles at this stage.

STAGE III

With the development of the second pair of opposite leaves at right angles to the first pair, and directly over the cotyledons, we have the third stage (fig. 22). At the insertion of each of these leaves, there starts to differentiate a single bundle, passing outward into the leaf, and downward through the stem, becoming inserted in the crotch of the fork of the bundle just developed at the close of the preceding stage (fig. 21).

If we now examine this latter bundle (fig. 23), we find that it possesses three protoxylem elements, one being derived from the newly developed trace of one of the second pair of leaves, the other two connecting, one through each of the horizontal connecting branches, with the outgoing leaf traces of the first pair of leaves. At the lower end of the bundles (figs. 24 and 25), one of the protoxylems passes out along one of the forks; the other two, which have been closely applied to each other throughout the whole length of the bundle, pass out the other. These bundles at first have the appearance of being double, the two parts being separated by a narrow parenchymatous (medullary?) ray, but being, later at least, entirely surrounded by a complete endodermis.

A cross-section (fig. 28) through the middle of the second epicotylar internode shows an epidermis, or rather protoderm, of thin-walled cells, sharply marked off from the internal cells. Within this protoderm is a meristematic tissue of cells practically all alike, showing no differentiation into cortex and central cylinder,

and with no air spaces. In this ground tissue are imbedded the two procambial strands of the traces of the second pair of leaves.

In the middle of the node below, there is to be seen a ring of vascular tissue inclosing an area of rounded parenchymatous cells similar in appearance to the cortical cells surrounding the vascular tissue. The inner layer of the cortex differs from the remaining cortical cells only in being more tightly placed together, thus forming a sheath. There is as yet no thickening of the walls of the cells forming this sheath.

Immediately below this node, the sheath sinks in between the four bundles, breaks, the ends turn in and form a complete sheath around each of the bundles, inclosing also a small amount of the undifferentiated parenchyma (pith?) on the inner face of each bundle. This condition persists throughout the internode. At the forking of the two opposite side bundles (figs. 24 and 25), the sheath sinks in between the forks, and so forms a complete sheath around each branch. On entering the cotyledonary node, these sheaths break on the inner face of the bundles, open out, the ends of each fuse with those of the adjacent bundles, forming thus a complete, but at first irregular, sheath around the entire central cylinder of the hypocotyl, which sheath continues downward into the root. At places, the bundle sheaths in the basal epicotylar internode show the characteristic Casparian dots on the side walls; this is also true of the sheath around the central cylinder of the hypocotyl and root. At this stage, however, the sheath is extremely irregular, being often of two layers for a short distance, and in most places showing no special endodermal characteristics.

A cambium has appeared in the bundles from the first pair of leaves, but very little secondary tissue has as yet been formed. In the hypocotyl there is a much interrupted cambium which has formed a little secondary tissue. At a later stage, the cambium forms a complete ring, and so develops a complete ring of secondary vascular tissue. In the root there is now to be found an interrupted cambium, which later becomes complete except at the protoxylem poles. The older primary root, therefore, will have two crescent-shaped masses of secondary tissue, the horns of which come together opposite the protoxylem poles.

The buds, found at the preceding stage in the axils of the cotyledons, have developed somewhat, each having now two very small leaves, each of which furnishes a single trace which passes downward into the hypocotyl. These become inserted, one on each side of the cotyledonary trace, between it and an arm of the forked bundle entering from above.

The bases of the first pair of leaves were at first distinct, but they have by this time grown together to form a short tube. This is the case with all the later formed leaves. A bud is starting to develop in the axil of each of the first pair of leaves, but at this stage has developed no vascular tissue.

From now on, the order of differentiation of new bundles is the same as that just described. At the close of each stage, there develops a pair of opposite bundles, each double in appearance, having two groups of protoxylem and protophloem elements separated by a parenchymatous ray. These bundles fork below, the forks being inserted between the traces of the underlying pair of leaves and those of the latest formed pair. Above, the bundles fork, connecting with the outgoing, latest formed leaf traces. In the next stage, these bundles become surrounded by a sheath which finally develops into a well marked endodermis. At the beginning of each stage, there is differentiated a trace from each of the newly formed leaves, which trace passes downward to the node below, being there inserted in the crotch of the underlying forked bundle which has just been developed at the close of the preceding stage.

The central bundle

The earliest sign of any medullary vascular tissue is to be found in a single example of a fourth-stage seedling, where, in the first epicotylar node, there are traces of medullary phloem. The course and attachment of these medullary phloem strands (fig. 30) are best described by starting with the conditions found just below the node, and following these upward through the node.

As the four bundles found in the basal epicotylar internode spread out on entering the node to form a complete ring, three protophloem elements from the peripheral vascular tissue pass inward toward the center. One of these protophloems arises from

the side of one of the leaf traces of the first pair of leaves. This single protophloem element passes inward toward the center of the ring. It never reaches it, however, but turns upward, and disappears in the middle of the node. The other two protophloem elements arise, one from the side of the other leaf trace, and the second from the adjacent face of one of the side bundles. These pass toward the center, become applied to each other, and pass vertically upward for a short distance; one disappears, the other soon turns, and passes back to that side of the stem on which it arose, becoming inserted, at the top of the node, on one of the "forks" on the side nearest one of the descending traces of the second pair of leaves.

In a very similar case found in a fifth-stage seedling, a single protophloem passes off toward the center from each side of each leaf trace. These four protophloem elements pass toward the center and turn upward, then turning back to the ring, each fuses with one of the descending forks, just as these enter the ring at the top of the node. In these two cases, the medullary vascular tissue is all entirely intranodal, there being no trace anywhere except just within the one node.

In the fifth stage, however, there is usually developed the central bundle of both xylem and phloem, passing from one node to the next. There is considerable irregularity in its formation, some of the fifth-stage seedlings being entirely without any medullary vascular elements. Taking a seedling where the central bundle has developed, we find, at the third node back from the apex, an elliptical vascular ring surrounded by a well marked sheath which usually, at this stage, does not possess any special endodermal characters. There is no sign of any internal endodermis in this node.

In passing downward out of this node, just as the vascular ring breaks up into four bundles, from one edge of one of the side bundles, a small group of phloem and xylem elements passes inward, free from the outer ring, to the center of the pith, meeting there another group of vascular tissue, which has broken off from the other end of the same side bundle. At a more mature stage, the medullary bundle may be derived from four sources, one at each end of each of the side bundles.

At this stage, the oblique cross-arms are imbedded in the parenchymatous tissue, there being no trace of any sheath. After turning so as to pass vertically downward, the fused bundles become surrounded by a more or less well marked sheath, which soon shows the characteristic Casparian dots on the side walls of the cells. Just above the node below, most of the vascular elements have died out, there being left only three or four phloem elements. These lose their surrounding sheath, and pass across to the peripheral vascular bundles at a level where the endodermis surrounding the forks has just broken. The medullary vascular tissue becomes applied to the outer side of one of the forks, on the opposite side of the stem, however, from which it branched off at the node above. Soon after this the nodal ring becomes closed. If we examine closely the upper node, we find that the vascular elements which turn in to form the central bundle may be traced through the node into the forks of the side bundles of the overlying internode.

At the next stage, the central bundle is differentiated in the next internode above in the manner just described, the lower end of this new bundle becoming inserted at the top of the older central bundle between the incoming cross-arms. A cambium makes its appearance in the central bundle and cross-arms about two stages after the differentiation of these bundles. This cambium frequently forms a more or less complete ring. Usually, however, in the seedling stages, the primary xylem and phloem crowd over to one side of the bundle, the cambium coming in as an arc, forming a collateral bundle of exactly the same structure as the peripheral bundle, in spite of its entirely different origin.

The internal endodermis

In the first five stages, the endodermis which surrounds the bundles throughout the internodes disappears from the inner faces of the bundles on reaching the nodes, leaving only an endodermal sheath surrounding the vascular ring in the node. From the sixth stage on, however, it is usual for the endodermis to be continuous through the node, both externally and internally.

Taking an older node as a type, we find (fig. 3), just above the node, that every bundle is surrounded by a regular endodermal sheath. The leaf trace sheath is usually well differentiated only

on the abaxial side. The sheaths of the two bundles between which the leaf trace enters soon open, the ends becoming connected so as to form a complete sheath around the two bundles and the leaf trace (fig. 4). The inner face of the sheath now bulges toward the central bundle, finally coming in contact with it, and breaking at the point of contact, thus forming a continuous sheath inclosing a dumb-bell-shaped area, each head consisting of the leaf traces and the two side bundles of the stem, the central bundle in the middle of the connection. The endodermis on each side of each "head" now bulges toward the remaining pair of stem bundles, coming in contact with the endodermal sheaths of the latter, and breaking at the point of contact.

There are thus formed three complete rings of endodermis (fig. 5), one externally surrounding the vascular ring, the other two internal, one on each side of the transverse connecting arms. These connecting arms very soon break, the endodermis sinking in so as to form one sheath around the central bundle, and another lying just internal to the vascular ring (fig. 6). This vascular ring now breaks into four parts, the endodermis sinking in until the external and the internal sheaths meet, then breaking apart, thus forming the four bundles of the lower internode, each surrounded by a complete endodermal sheath (fig. 9).

Late stage of seedling

As has been said, the seedling, by the end of the growing season, attains a height of about 2 dm. Such a plant (fig. 31), possessing about 20 nodes, looks very much like a plant of the "mature" type, but is smaller than the mature plant, and of course differs in not having arisen from a rhizome. At the base, several of the axillary buds have developed to form short, nearly horizontal branches, the rhizomes. At the very base there is a cluster of four strongly developed adventitious roots, nearly surrounding the primary root, which is still less developed than the adventitious roots.

A histological examination shows that the vascular system has developed in the manner already described. The uppermost pair of leaves furnish a single trace each; these pass downward to the

second node, where there has been formed a vascular ring. On passing through this node, we now find a new condition. Instead of the vascular ring breaking into four bundles, two of which fork lower down in the internode, it breaks into four bundles, two of which almost immediately divide, the four forks behaving in the same way, however, as the forks produced at the lower end of the internode of earlier stages (see diagram of path of bundles, fig. 29). This condition is very nearly that which exists in the apex of a mature plant (compare diagram, fig. 2), where the nodal ring breaks up immediately into six bundles, four of which, corresponding to the two forked side bundles, are usually smaller than the other two.

An examination of the lower internodes of this stage (fig. 29), or of the corresponding internodes of the intermediate stages, shows that there is a tendency from the very first for the side bundles to fork at a slightly higher level in each succeeding internode. In the third stage, where these side bundles first come in, there is but a very small amount of parenchymatous tissue inclosed above the leaf traces by these forks, forming small leaf gaps. At each succeeding stage, these gaps tend to be longer when formed. I say tend, for there is considerable irregularity. One of the side bundles may fork about the middle of the internode, while the opposite side bundle of the same internode may not fork until very near the bottom of the internode, or, as before mentioned, may not even fork at all. In any individual seedling there is a gradual transition from the immature seedling condition found in the earliest stages, and hence lowermost internodes, to the nearly mature conditions found in the uppermost internodes of the seedling at the end of the growing season.

The old seedling shows, therefore, a permanent record of its ontogenetic development, slightly obscured, it is true, by secondary thickening. It is comparable in this respect to a fern "seedling," the earliest formed internodes showing the simple (primitive?) type of structure, the later formed ones showing a gradual transition to the mature type. It must be remembered, however, that in the fern, when the mature structure is once formed, the main axis continues its growth, each succeeding internode having the mature

structure. In *Dianthera americana*, on the other hand, the main axis seems never to produce a perfect mature type, but only approaches it. The mature type is here first produced in a branch, the rhizome. When once attained, however, it is persistent, as in the case of the fern.

Owing to the secondary development of vascular tissue, the general appearance of the bundles, or meristeles, has changed considerably. Instead of being strictly collateral, as they were in the earlier stages, there is a tendency for them to become concentric, the xylem and phloem being formed on the sides, and later, by the extension of the cambium, they are also formed on the inner face of the meristeles. The cambium may even form a complete ring, though this is not common in the seedling stages.

The presence of this internal, and of course, inversely oriented mestome, causes the node of an older seedling to have a rather different appearance from that of the young seedling. On entering the node (figs. 3–9), part of the vascular tissue on the sides of the meristeles, sometimes of the phloem only, sometimes of both xylem and phloem, passes around to the inner face, becoming inverted during the passage. Part of the internal mestome of two of the bundles turns into the transverse arm, and so connects with the central bundle. Below the transverse arm there are three concentric rings of endodermis, one external to the complete ring of normally oriented xylem and phloem, the second just within the inversely oriented mestome. The third and innermost endodermis surrounds the central cylinder. The normally oriented mestome is separated from the inverted vascular tissue by a layer, several cells in thickness, of closely packed parenchymatous cells. This layer is continuous with the parenchyma of the individual meristeles, above and below the node. The middle endodermis is separated from the innermost sheath by a layer of cells continuous with the ground tissue of the internode, but much more closely packed together. There is, however, still a considerable amount of air space.

The epidermis and ground tissue of the late seedling are exactly like those of the mature plant. As HOLM has already accurately described and figured these tissues, nothing more need be said of

them. The leaves of the seedlings correspond very closely to those of the mature plant. The latter have been fully described by HOLM. One correction must be made, however. HOLM says (5, p. 326) "collenchyma and stereome seem to be entirely absent from the lateral portion of the blade," apparently overlooking the marginal strand of collenchyma occuring in both seedling and adult leaves (fig. 32).

The axillary buds

It has already been mentioned that buds are usually formed in the axils of the leaves. In most cases, except at the base of the plant, these buds, after having developed one or two pairs of very small leaves, remain dormant. Several of the basal buds may develop, giving rise to the horizontal rhizomes, by means of which the plant perennates. The bud arises as a small mound of tissue in the axil of the leaf. On this mound there soon appear the primordia of a pair of opposite leaves, whose plane of symmetry is at right angles to that of the subtending leaf. A single leaf trace from each leaf is differentiated, and passing downward becomes inserted between the trace of the subtending leaf and an arm of the forked bundle of the stem.

As in the main stem, the next step in development is the differentiation of a pair of forked bundles, the forks of the outer bundle being inserted between the first pair of leaf traces and the trace of the subtending leaf. The arms of the other forked bundle become inserted behind the first pair of leaf traces, between them and the forks of the stem bundle. As in the stem, a pair of traces from the second pair of leaves now differentiate, and become inserted in the crotch at the top of the forked bundles. By this time it is seen that a very irregular sheath is forming around each of the bundles of the lower part of the bud (fig. 33). On entering the node below, these sheaths open on the inside, the ends connecting so as to form a complete sheath surrounding the bundles of the bud and the trace of the subtending leaf (fig. 34). Lower down, this sheath opens on the inside, the ends connecting with those of the opening sheaths of the "forks" of the stem. This forms a complete sheath around all of the bundles, as is shown in fig. 35. The endodermis now behaves in the way already described in a node which had no bud.

The later development of the axillary bud is exactly the same as that of the main stem, with this exception: while in the stem the transition from seedling structure to the mature type is very gradual, the transition in the branch is much more rapid, being completed in about 6–8 internodes. After having once been attained, the mature type recurs constantly in each succeeding internode.

Roots

In the old seedling there are to be found four types of roots, each having its characteristic structure. These are the primary, secondary, and adventitious roots, and the branches of the latter.

The primary root is diarch, maintaining this type of symmetry even when mature. Its growing point is of the "*Helianthus*" type, having distinct plerome and periblem initial groups, while the calyptrogen and dermatogen have a common group of initials. As the root matures, a cambium develops in a ring, broken opposite the two protoxylem poles, forming two crescents of secondary vascular tissue. The stele is surrounded by a sharply defined thin-walled endodermis with Casparian dots. The cortex and epidermis correspond to those of the adventitious roots of the mature plant, sufficiently described by HOLM. He, however, wrongly calls these roots "secondary" (**5**, p. 319).

The true secondary roots, that is the branches from the primary root, possess the same type of growing point as the primary root. The symmetry varies with the age, the younger parts of these roots being usually diarch, and becoming later tetrarch or pentarch. The general structure of these mature secondary roots is that of the adventitious roots. The adventitious roots, formed at the base of the seedling, and the branches of these adventitious roots, are exactly like those described by HOLM for the mature plant. These also possess the "*Helianthus*" type of growing point.

Abnormalities in the internal structure

One very striking feature about the seedlings of *Dianthera americana* is their extreme variability. Two seedlings of the same stage, that is with the same number of leaves developed, may show very great differences in the degree of differentiation of vascular tissue, cambium, endodermis, etc. For instance, a seedling of the

fifth stage may have a better developed endodermis in its basal internode than can be found in an ordinary seedling of the eighth or ninth stage.

One of the most striking abnormalities, however, is the failure of an entire bundle to differentiate. This is frequently the case with the central bundle. This may develop in one internode, fail to do so in the next, may or may not develop in the next, and so on. A couple of examples may be given. Counting the internodes back from the apex, one never finds any trace of medullary vascular tissue in the first and second internodes (the apical meristem, being above the first node, is of course not counted). The central bundle normally develops in the third internode, and it may be developed in all of the nodes below this. An abnormal seedling of the ninth stage shows the bundle developed only in the seventh internode from the top, being entirely absent elsewhere. An abnormal seventeenth-stage seedling (near the end of the first growing season) shows the central bundle only in the third, fourth, fifth, seventh, eighth, twelfth, thirteenth, and fifteenth internodes.

Abnormalities in the peripheral bundles are less common. The failure of a side bundle to fork at the bottom of the internode has already been mentioned. In a single case of a mature seedling, another type of abnormality was found. In one of the basal internodes, the forks of one of the side bundles, undoubtedly normal in its younger state, had grown together at the base, owing to the large amount of secondary thickening. In the upper part of the internode there is a single bundle which forks normally, the forks coming together, however, at the base, the endodermis disappearing between them. As the leaf trace enters, the endodermis opens upon the outside and forms a complete sheath around the trace and the fused bundle, the latter opening just enough to allow the trace to be inserted between its halves.

In the basal internodes of the branches, there are usually four peripheral bundles. Rarely, however, one of the side bundles fails to be differentiated.

The mature plant

At the close of the growing season, the rhizomes produced at the base of the seedlings have developed the mature type of structure in their younger internodes. Growth now practically ceases, the

main axis of the seedling dying down. At the beginning of the next growing season, the growth of the plant is continued by the rhizomes, the apices of these turning upward as they grow, to form the aerial shoots, each internode of which contains one central and six peripheral bundles, each surrounded by a complete endodermis. The development of these internodal structures is exactly that which has been described for the seedling.

Passing back from the apex (see diagram, fig. 2), one finds at the second node a vascular ring, which just below the node breaks immediately into six bundles. As in the seedling, there is no differentiation of a sheath in this (second) internode. In the next node, however, a sheath appears, surrounding the vascular ring. Below this the sheath sinks in around the six peripheral bundles. An irregular sheath also appears around the central bundle, which first shows in this (third) internode. The internal endodermis passes through the next node in the manner already described in an old node of the seedling (figs. 3–8).

A cambium develops in the pair of bundles entering the stem from the leaves in the second internode from the apex. It appears in the side bundles in the next lower one. This cambium at first forms an incomplete ring, but in the older internodes it is frequently complete. The concentric structure thus produced, of pith surrounded by xylem, phloem, and a stereomatic pericycle, the whole surrounded by a sharply differentiated endodermis, certainly justifies HOLM'S statement (**5**, p. 309) that "in *Dianthera* the steles are very distinct and readily to be recognized as such, since they are cylindric and possess all the necessary elements."

The central bundle in the mature plant is plainly derived from vascular tissue passing downward from the four side bundles (figs. 2–7). As in the seedling, it arises first in the third internode, cambium usually showing in the fourth. The mature central bundle, as HOLM has described, usually has the appearance of being double, the mestome forming two arches, with parenchyma between, the whole surrounded by a well marked endodermal sheath.

The mature type of vascular structure seems to be rather constant. HOLM mentions that the central bundle may sometimes be lacking, but an examination of several hundred internodes of mature plants has failed to show such a condition. One single

internode, lying between two normal ones, showed three medullary bundles, the central one like the one ordinarily found, one a collateral bundle surrounded by an endodermis in structure therefore like one of the peripheral meristeles. The third, also surrounded by an endodermis, was a strictly concentric bundle, with no parenchymatous tissue, the protoxylem in the center, surrounded by a complete ring of xylem, cambium, and phloem.

The anastomosing of the bundles in the mature plant has already been described (fig. 1). Sections show that the minute vascular structure is very similar to that found in an old node of the seedling. Frequently, however, there is more of the inversely oriented vascular tissue. Some of the vascular elements on the sides of all six of the peripheral bundles may pass around to the inner face just before entering the node, and so become inverted.

HOLM, in speaking of the node, says (**5**, p. 323) "from the union of these steles each of the two opposite leaves receives three mestome cylinders, readily observed in the petiole as one central, very broad, and arch-shaped cylinder, with a much smaller one on either side." From the anastomosing bundles there is given off only one single trace to each of the leaves. This single trace, however, while passing through the cortex, gives off a branch on each side, so that each petiole does receive the three bundles as described by HOLM. This giving off of a single leaf trace, which trifurcates while yet in the cortex, is, according to VAN TIEGHEM (**11**), the conformation found in all of the Acanthaceae. It should be noted, however, that DEBARY (**3**, p. 243), in speaking of the course of the bundles in the stem, places *Ruellia maculata* in the group described as having "leaves opposite: traces of three or four bundles, which unite at the second lower node with those of the next lower pair: not pectinated."

The leaves of the aerial shoot have already been fully described by HOLM. In structure they are identical with those of the seedling, hence the correction concerning the presence of the marginal strand of collenchyma in the blade has to be made here also.

The axillary buds of the mature plant

As in the seedling, a bud is usually formed in the axil of each leaf. Those at the base of the aerial shoot usually develop into rhizomes, or more rarely into vertical aerial branches. In either

case, the development is exactly the same as in the buds of the seedling, having therefore an astelic structure. Each internode has six peripheral and one central bundle, except the basal, in which the central bundle may or may not be differentiated.

The buds of the upper part of the plant, on the other hand, ordinarily develop into inflorescence axes. As HOLM has pointed out, these have a monostelic structure (fig. 36). These buds start their development in the same way as do the buds which develop the rhizomes and stem branches. The first pair of leaves, or rather bracts, first furnish a pair of traces, then the pair of forked bundles develop; the second pair of bracts supply a pair of traces, exactly as in the other kind of bud. The connections of these bundles with each other and with those of the stem on which they are inserted are also as in the branch bud. The pedicel of the single flower developed in the axil of each bract possesses a ring of vascular tissue. At the base this ring splits on the face nearest the bract on one side, and nearest the inflorescence axis on the other. The two halves so produced become inserted between the bract trace and the forked bundle of the inflorescence axis.

The difference between the structure of the inflorescence axis buds and those forming ordinary branches soon becomes visible. One difference is the greater length of the internodes of the latter. The most important difference between them, however, lies in the fact that in the inflorescence axis, the inner layer of the cortex, while forming a rather irregular sheath around the stele, apparently never forms a strongly developed endodermis. This sheath, on passing out of a node, never sinks in between the bundles, but remains as a ring, marking the boundary, rather indistinct at times, between the cortex and the central cylinder. The parenchymatous tissue of the latter differs from that of the former in being made up of larger cells, and in containing a very much smaller proportion of air space. The general appearance of a cross-section is very similar to a monostelic stem in which the individual bundles tend to remain separate.

Let us now compare the insertion of a well developed branch with that of an inflorescence axis. Taking a case where the basal internode has no central bundle, we find that the trace of the subtending leaf enters between the abaxial side bundles of the branch.

The endodermal sheaths of the six branch bundles open up, each connecting with that of the adjacent bundles, so as to form a complete sheath around the leaf trace and the six branch bundles (figs. 33–35). Where the central bundle is present, a connection is made between the two pairs of side bundles and the central bundle, all of the vascular tissue of the latter passing to the periphery and becoming normally oriented. Then the ring of the six peripheral bundles and the incoming leaf trace become surrounded as before by a common sheath (figs. 37–41).

In the case of the inflorescence axis, the vascular ring shows a tendency to break up into six bundles. This ring opens on the side to allow the entrance of the leaf trace, or rather bract trace; the sheath then surrounds the ring and the trace (figs. 42–45). The structure so produced is in cross-section almost identical with that produced by the branch. The further history is the same for both types.

The organogeny of the flower

The apex of the inflorescence axis continues its activity all through the flowering season, giving rise to opposite, decussate bracts, in the axils of which are produced the flowers. The greatest growth of the inflorescence axis is due to intercalary activity in the basal internode.

In the axil of each developing bract a slight mound develops. On this mound, which is to be the flower, there appear first of all, apparently synchronously, the five sepals (fig. 46), followed very soon by the five petals. At first the latter are separate, but soon coalesce to form the corolla tube. About the same time that the corolla is initiated, two large mounds appear, marking the primordia of the stamens (figs. 47 and 48). There is never any trace of more than two stamens (five occur in some of the Acanthaceae, in other genera there are two stamens and three staminodia). The ovary grows up as a ring (fig. 49), the sides nearest and farthest from the axis of the plant being slightly (10–15 μ) higher (fig. 50). The petals soon coalesce, the stamens being carried up on the corolla tube. The ovarian "ring" closes in over the top and continues its growth to form the pistil with its deeply two-lobed stigma. The placentae grow out from the opposite walls of the ovary, near its base. Two ovules arise on each placenta. The two placentae now gradually

grow together, dividing the ovary into two cells. One ovule from each placenta is left in each cell.

The vascular supply of the floral organs

In the pedicel of a mature flower is to be found a complete ring of vascular tissue. Above this ring breaks up into 26 bundles, three of which pass out to each of the five sepals, five bundles passing up into the tube of the corolla, two large concentric bundles supply the stamens, and four pass up into the ovary. Two of the latter bundles, lying in the sagittal plane of the flower, pass up the carpellary walls, each giving off two laterals. The laterals die off near the top of the carpel, the medians however passing out into the style, which therefore possesses two bundles. The two remaining carpellary bundles branch, each giving off a bundle which supplies the placental wall. The other arm of each forks, the bundles so produced passing up the side walls of the carpel until near the top, where they disappear. Each of the five bundles passing out into the tube of the corolla gives off several branches while passing through the tube. Each of the stamen bundles pass up between two of the bundles of the corolla, being sharply distinguished from them in being concentric instead of collateral. They pass out into the stamens when the latter become free from the corolla tube.

As we pass down the short pedicel to its insertion, we find the ring first opens on the inner face (figs. 51 and 52). The inflorescence axis shows two large flat bundles, each of which now forks (figs. 51 and 52), each of the arms becoming applied to the sides of the opened ring from the pedicel (fig. 53). These two vascular masses then divide to allow the entrance of the single bract trace. The two vascular bundles now tend to round up (fig. 54). In the basal internode this division into two parts is not so marked, as the endodermal sheath usually forms a complete ring around the vascular tissue (fig. 36).

Discussion

According to HOLM, some of the species of *Dianthera* which he examined were monostelic. These were *D. comata* L., *D. glabra* B. & H., *D. inserta* Brandg., *D. ovata* Walt., *D. parvifolia* B. & H.,

D. pectoralis Murr., and *D. sessilis* Gray. I was unable to obtain any of these species for comparison. I did obtain seeds, however, of the fairly closely related *Justicia ventricosa*. A few of these germinated, and I was able to study a few of the seedling stages. The germination is similar to that described for *Dianthera americana*. Likewise are the first three stages. After that, the interfascicular cambium masks the primary structure.

Comparing this then with *Dianthera americana*, we find that they are at first exactly the same. The first point of difference is the failure of the interfascicular cambium to appear. This leaves the bundles separate, around which the endodermis turns in and surrounds, instead of remaining as a complete ring, as in *Justicia*.

In the mature plant, we find that the first two apical nodes of *Dianthera americana* are similar to other acanthaceous plants (*Justicia*, *Fittonia*, etc.). In the latter, the traces of the first pair of leaves pass down to a ring of vascular tissue. Below this node there are two arcs of tissue, each of which is evidently of three parts, showing three widely separated protoxylems. This internode, therefore, has a structure exactly like that of a young internode of the inflorescence axis of *Dianthera americana*. At the next node the opposite leaf traces enter between the two arcs. Below this node the original structure cannot well be made out, owing to secondary thickening.

It is evident that the seedling and the inflorescence axis of *Dianthera americana* show the primitive condition of the group, and that the formation of endodermal sheaths around each of the separate bundles, that is, the condition of astely, is a secondary condition, found only in a part of the species of *Dianthera* (according to Holm, *D. crassifolia* Chapm. and *D. lanceolata* Small, are also "polystelic").

Although astely apparently has not been previously described as occurring in the Acanthaceae, yet many other vascular abnormalities are known. The interxylary phloem of *Thunbergia* and others is well known. Intraxylary phloem (*Thunbergia*, *Hexacentris*, *Barleria*, etc.), medullary phloem (petiole of *Acanthus mollis*), and even medullary bundles (*Acanthus spinosus*, etc.), have also been described. It is thus seen that the family shows irregularities of vascular structure.

In *Dianthera americana*, the two chief types of abnormality found in the family occur, that is, the astelic condition and the medullary vascular tissue. The former is evidently not in any way dependent on the latter, since in the seedling the plant is frequently astelic when there is no medullary tissue developed.

In the terms of the stelar theory, *Dianthera americana* in its early stages is monostelic. In the young seedling the first endodermis differentiated, surrounding the nodal ring, corresponds to the inner layer of the cortex. The stem apex is rather broad and flat, but the three histogen layers of HANSTEIN can usually be made out. From the plerome is developed a central cylinder, all that is within the endodermis. The parenchyma of this stele corresponds, therefore, to pith and medullary rays.

This seems clear enough in the early stages of *Dianthera* and also in *Justicia*. In the latter this condition persists permanently; there is always a well marked cortex and central cylinder, with its pith. In the internode of *Dianthera americana*, on the other hand, an endodermal sheath about each bundle is initiated, passing around the bundle and inclosing on the inner face of the latter a mass of parenchyma. From our previous interpretation, this endodermis differentiates on the sides of the bundles from the parenchymatous cells of the medullary rays, and on the inner face from the pith itself. In such a case the endodermis surely cannot correspond with any morphological layer.

Now let us examine the fate of the parenchyma of the original central cylinder, that is, that derived from the plerome. That part which is inclosed within the endodermal sheath undergoes little change, while that outside the sheath gradually becomes so modified as to appear exactly the same as the cortical tissue. At this mature stage, then, there is no visible differentiation between the cortex and the pith, except within the endodermis. And yet we have seen that they had an entirely different origin, the one derived from the plerome, the other from the periblem. Unless one leaves out of account the different origin, and compares only the mature structures, one is certainly not justified in saying in this case, as VAN TIEGHEM and DULIOT (**12**, p. 275) say in their definition of astely, that the bundles are "directement plongés dans la masse

générale du corps qui ne se séparé pas alors en écorce et conjonctif" (p. 275).

STRASBURGER (9) distinguishes between the inner layer of the cortex, which is a morphological layer, and the endodermis, which is merely "an air-tight barrier which does not prevent the passage of water through its cells. Such a layer is found in a position to shut off the water-conducting system of a plant from its air-containing lacunar system, but this position may vary within the same genus, and has no necessary connection with any morphological region" (quotation from TANSLEY 10).

According to this interpretation of the endodermis, which is therefore merely a physiological layer, astely is merely a modification of monostely. This is the view already taken by STRASBURGER (9); the same idea is presented in a recent paper by GRÉGOIRE (4). The parenchyma of the central cylinder, that is, outside of the endodermis, becomes different from that inclosed within the sheath, owing to the different physiological environment, and it becomes, like the cortical tissue, a response to the same physiological conditions.

If we leave out of account for the present the surrounding endodermis, we see that the medullary system of *Dianthera americana* corresponds to what COL (1), in his work on the arrangement of bundles, calls "série M'." He defines this type as follows (p. 242): "faisceaux normaux rentrant dans la moelle de la tige. Ils s'accolent inférieurement à d'autres faisceaux medullaires, et tous ceux des entre-nœuds les plus inférieure de la tige se poursuivent et se terminent isolément dans la racine (dans le bois) ou à la base de la tige."

WEISS (14) has shown that all medullary bundles of the stem are foliar bundles. The work of LIGNIER (7), KRUCH (6), and COL (1, 2) fully confirms this. In *Dianthera americana* it is easy to follow the leaf trace downward through two internodes, and to see that a part then turns inward to form the medullary vascular tissue.

In a paper describing for the first time the medullary bundles of *Acanthus spinosus*, VESQUE (13) says that he thinks the primary effect of the internal position of the phloem is its very efficacious

protection. He calls attention to its common occurrence in lianes and in creeping plants, and says that the protection counterbalances the danger to the phloem due to the great length and weakness of the stem.

COL (2), on the other hand, presents the following hypothesis (translated from p. 275): "The histological structure of the conductive tissues does not permit a sufficient condensation to form a single circle. The wood becomes condensed, more easily than the phloem, into a small bundle; without doubt on account of the fluidity of the ascending sap, and of the easy passage of liquids from one vessel to another. For converse reasons, the phloem is less capable of becoming condensed." When two bundles come together, therefore, the phloem passes around the sides of the wood to the inner face, or it may even become medullary. While it is undoubtedly true that the phloem is better protected in its internal position, as suggested by VESQUE, yet from my observations on *Dianthera americana*, it would seem that the hypothesis of COL certainly holds in that plant.

It may be that, in this case, the internal vascular tissue is correlated with the lack of a complete ring of vascular tissue. The phloem, not finding sufficient room on the outer face of the individual bundles, becomes crowded around to the sides, or even to the inner face of the bundles. The new vascular tissue descending from the uppermost leaves does not find room for its insertion, so part of it at least passes inward to form the central bundle. After it has begun its development imbedded in the pith, a sheath finally differentiates to separate it from the air-containing tissue of the much modified mature pith.

As to the cause of the astelic conditions found in this and other species of *Dianthera*, very little can be said. It is probably correlated, however, with the aquatic habitat. The large amount of air space undoubtedly is to be correlated with the aquatic habitat. If we agree that the endodermis is not a morphological boundary, but a physiological layer separating the vascular tissue from the "air-containing lacunar system," as claimed by STRASBURGER, then we have a simple, plausible explanation of this phenomenon.

More comparative work on this and other species of *Dianthera*

is needed, however, especially to find out if possible the physiological value of the endodermis. Possibly such work would lead to the discovery of the reason why some species of this genus are monostelic, and apparently normal in every way, while other species are abnormal in being astelic, and in possessing medullary vascular tissue.

Summary

The mature plant of *Dianthera americana* is astelic, instead of polystelic, as claimed by HOLM. It possesses six peripheral meristeles and one central medullary bundle, each completely surrounded by an endodermal sheath. At the nodes these anastomose.

The seedling is at first monostelic; the individual bundles gradually become surrounded by the endodermal sheaths.

The mature type of structure with six bundles is derived from the seedling type with only four, by the increase of the size of the leaf gaps.

The inflorescence axis is monostelic.

Dianthera americana differs from related forms in the lack of interfascicular cambium, the individual bundles becoming surrounded by endodermis. Its medullary bundle is quite comparable to the medullary bundles of *Acanthus spinosus*, many Campanulaceae, and other plants.

It is probable that astely is merely a phase of monostely, the endodermis being a physiological layer, the medullary and cortical parenchyma becoming similar owing to like physiological conditions.

Astely in this plant is probably correlated with its aquatic habitat.

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EXPLANATION OF PLATES I–IV

All drawings of sections were made by means of a camera lucida. In the diagrams, xylem is represented by cross-hatching, phloem by dots. In figs. 3–9 the endodermis is represented by cells. The index letters are as follows: *A.R.*, adventitious root; *B*, bract; *BR*, branch; *BR.T.*, branch trace; *C*, carpel; *C.B.* central bundle; *CL*, calyx; *COT*, cotyledon; *CR*, corolla; *END*, endodermis; *EP*, epidermis; *ESP*, endosperm; *I.A.*, inflorescence axis; *L*, leaf; *L.T.*, leaf trace; *M.PH.*, medullary phloem; *P.B.* peripheral bundle; *PC*, procambium; *PPH*, protophloem; *P.R.*, primary root; *PX*, protoxylem; *S*, stamen; *ST*, stem; *T*, testa; *T.A.*, transverse arm.

PLATE I

FIG. 1.—Reconstruction of the vascular system of two adjacent mature nodes.

FIG. 2.—Diagram of the paths of the peripheral bundles of a mature stem.

FIGS. 3–8.—Series of successive transverse sections through a mature node, passing from fig. 3, made just at the top of the node, to fig. 8, made just below the node; ×45.

FIG. 9.—Transverse section through the upper part of an internode of an old seedling, showing one central and four peripheral bundles; ×45.

FIG. 10.—Part of a sagittal section of a seed, directly opposite the micropyle, showing the testa with its thickened epidermal cells, and the endosperm of two layers; ×185.

FIG. 11.—Sagittal section of a seed; ×12.5.

FIG. 12.—Longitudinal section of a seed, made perpendicular to the plane of the section shown in fig. 11, and through the line *mn;* ×12.5.

PLATE II

FIG. 13.—Transverse section of the upper part of the hypocotyl of a ripe seed, just below the insertion of the cotyledons; ×185.

FIG. 14.—Transverse section through the middle portion of the same hypocotyl, showing the periclinal division of the endodermis on either side of the stele; ×185.

FIG. 15.—Habit sketch of a seedling, stage I, with cotyledons still inclosed within the testa; ×1.5.

FIG. 16.—Transverse section of the upper portion of a first-stage seedling, just below the insertion of the cotyledons, showing the two "double" cotyledonary traces; ×185.

FIG. 17.—Diagram of the paths of the bundles in a seedling, stage I.

FIG. 18.—Diagram of the paths of the bundles in a seedling, early phase of stage II.

FIG. 19.—Habit sketch of a seedling, stage II (late phase); ×1.

FIG. 20.—Diagram of the paths of the bundles in a seedling, late phase of stage II.

FIG. 21.—Diagram of the paths of the bundles in a seedling, early phase of stage III.

FIG. 22.—Habit sketch of a seedling, stage III; ×1.

FIG. 23.—Transverse section of one of the side bundles in the basal epicotylar internode of a third-stage seedling, showing its "double" appearance, the three protoxylem, and three protophloem elements; ×380.

FIG. 24.—Transverse section of the same bundle as shown in fig. 23, at a lower level, just at the top of the fork; ×380.

FIG. 25.—Transverse section of the same bundle still lower down, the forking complete; ×380.

FIG. 26.—Surface view of a glandular hair; ×380.

FIG. 27.—Longitudinal section of a glandular hair and neighboring epidermis; ×380.

FIG. 28.—Transverse section of the uppermost internode of a third-stage seedling, showing the two procambial bundles of the traces of the uppermost pair of leaves imbedded in the ground meristem; ×380.

FIG. 29.—Diagram of the paths of the peripheral bundles in a seventeenth-stage seedling (near end of growing season), showing the gradual development of the "mature" type by the increase in length of the leaf gaps.

PLATE III

FIG. 30.—Restoration of the vascular system of a node of a fourth-stage seedling, showing the courses and attachments of the intranodal medullary phloem strands.

FIG. 31.—Habit sketch of an old seedling (stage XVII), near end of growing season, showing the development of rhizomes from the basal axillary buds; ×0.5.

FIG. 32.—Transverse section of the margin of the blade of a mature leaf, showing the collenchymatous strand; ×210.

FIGS. 33–35.—Series of successive transverse sections through the upper part of a node, showing the insertion of a branch which has no central bundle developed in its basal internode.

FIG. 36.—Transverse section of the stele of the basal internode of a mature inflorescence axis; ×45.

FIGS. 37–41.—Series of successive transverse sections through the upper part of a node, showing the insertion of a branch in which the central bundle has developed in the basal internode.

PLATE IV

FIGS. 42–45.—Series of successive transverse sections through the upper part of a node, showing the insertion of an inflorescence axis; ×50.

FIG. 46.—Longitudinal section through the apex of an inflorescence axis, showing the origin of the opposite bracts, the axillary flowers, and the primordia of the calyx on the lower flowers; ×50.

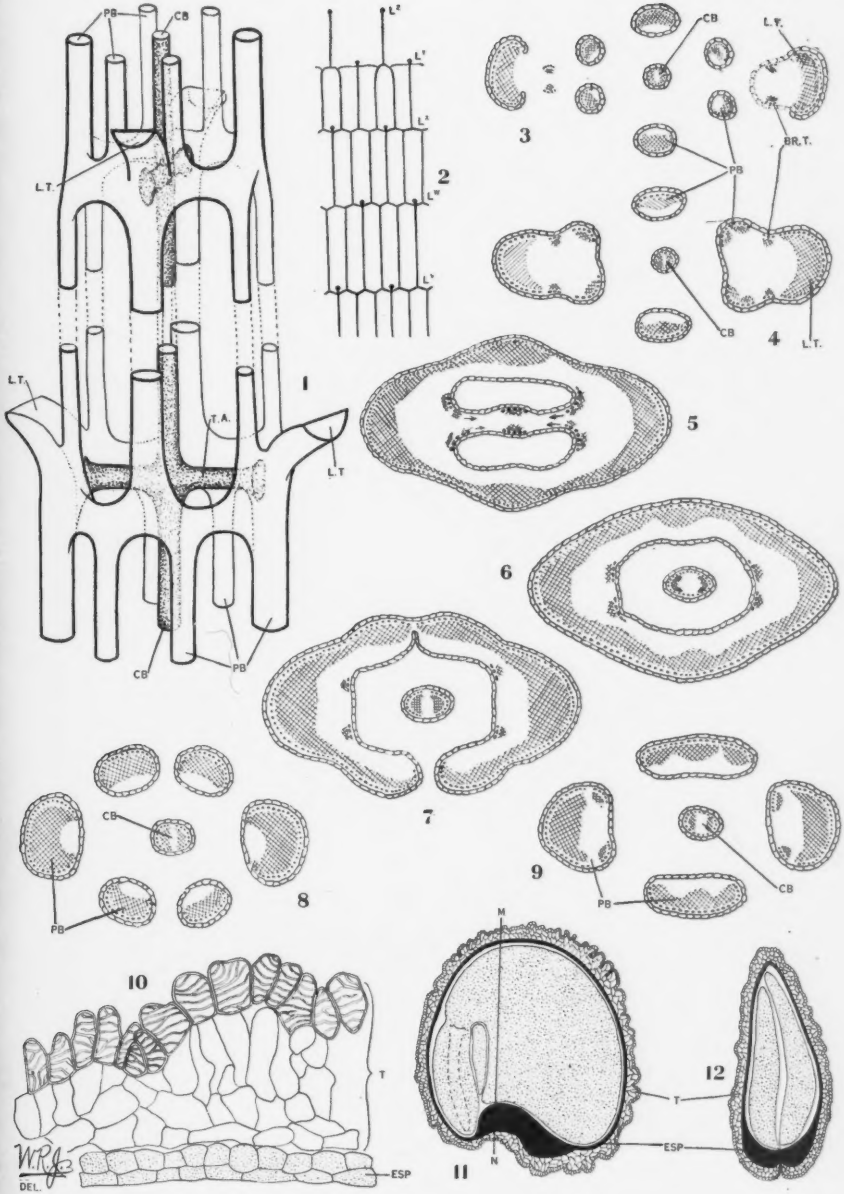
FIG. 47.—Longitudinal section of a young flower, not quite median, showing the bract, calyx, corolla, one of the stamens, and the edge of carpel; ×50.

FIG. 48.—Longitudinal section of a young flower, made perpendicular to that shown in fig. 47, along the line *mn*, showing the two large stamens free from the corolla; ×50.

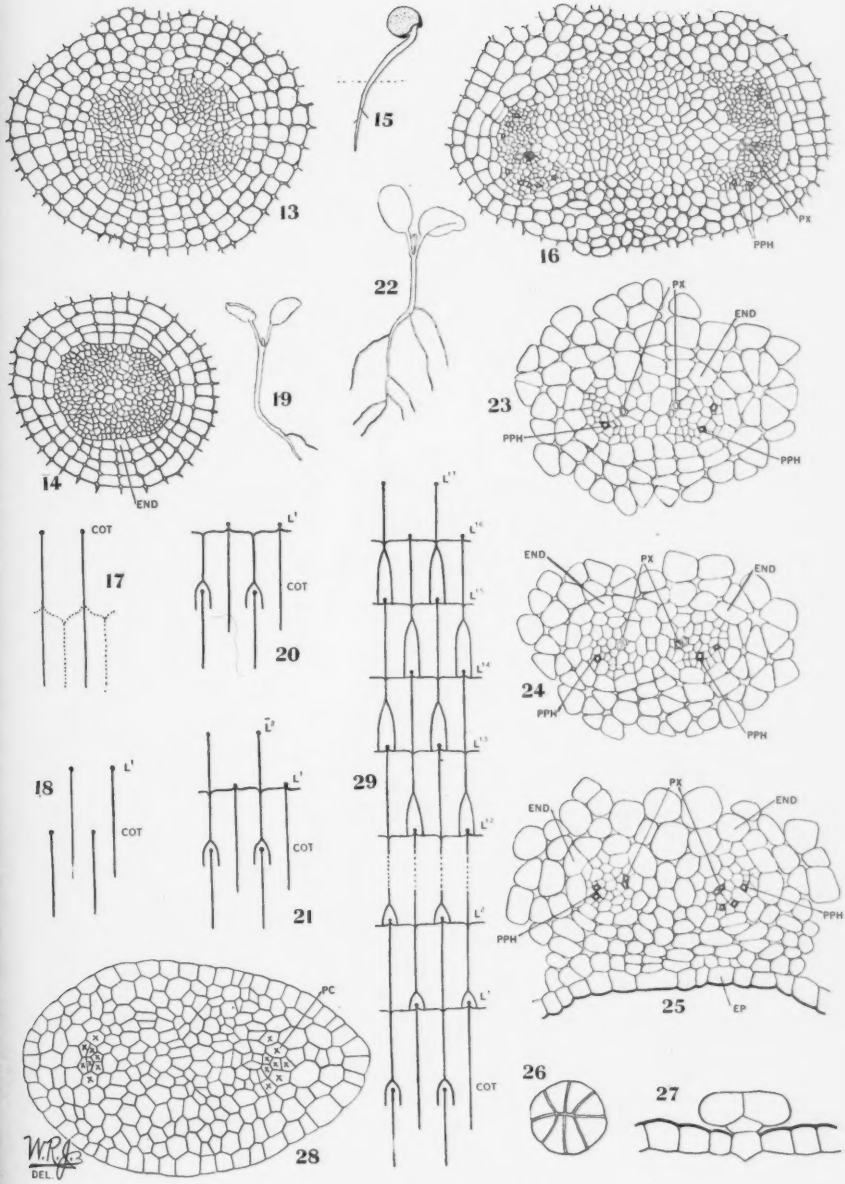
FIG. 49.—Sagittal section of a slightly older flower, showing the formation of the ovarian cavity; ×50.

FIG. 50.—Transverse section (very slightly oblique) of a flower of about the same age as that shown in fig. 49, showing the arrangement of the floral parts, and the two lobes of the carpels; ×50.

FIGS. 51–54.—Series of successive transverse sections through a node of an inflorescence axis, showing the insertion of the bundles of the opposite pedicels and bracts with those of the main axis; ×22.5.



JONES on DIANTHERA



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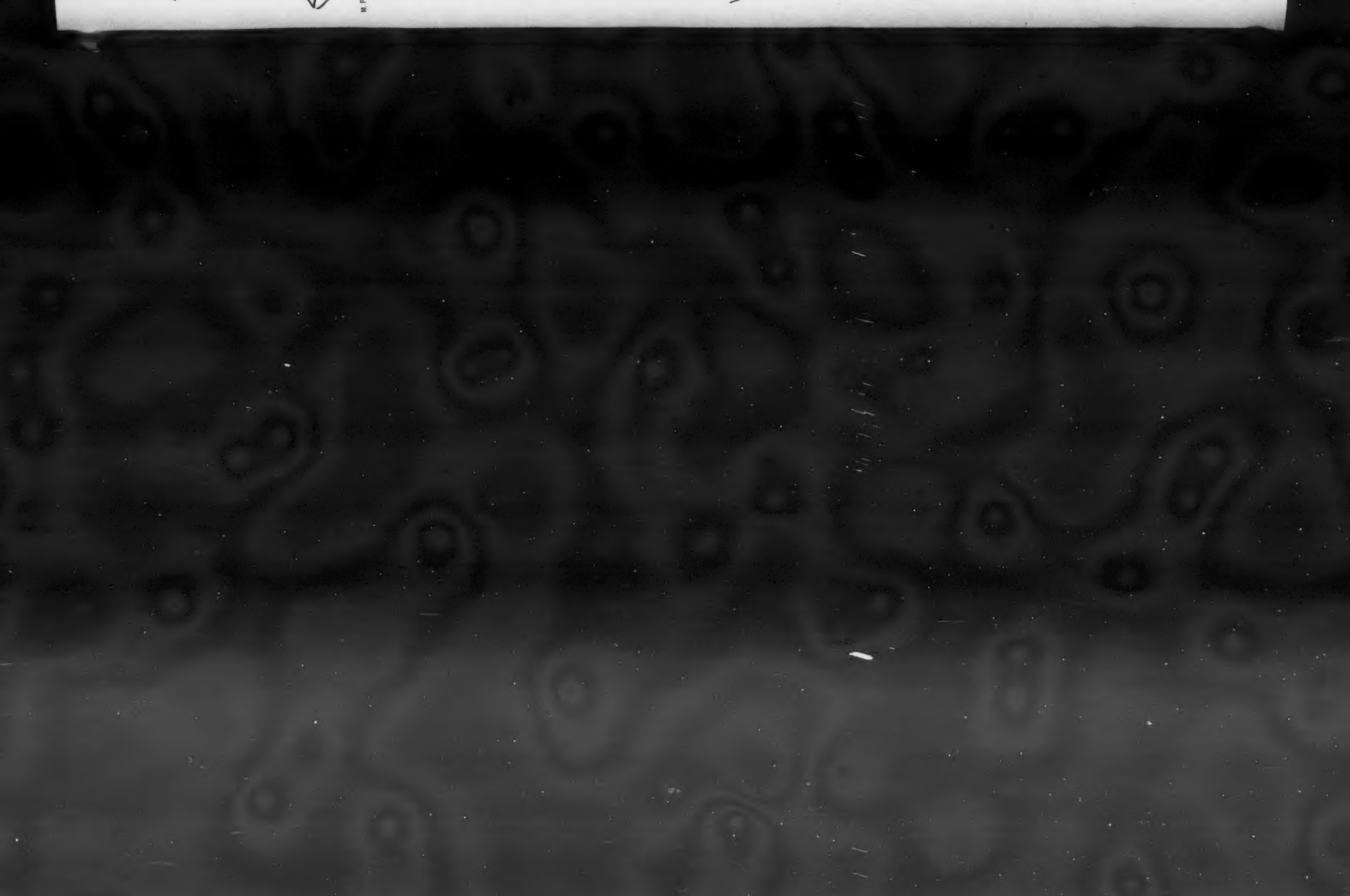

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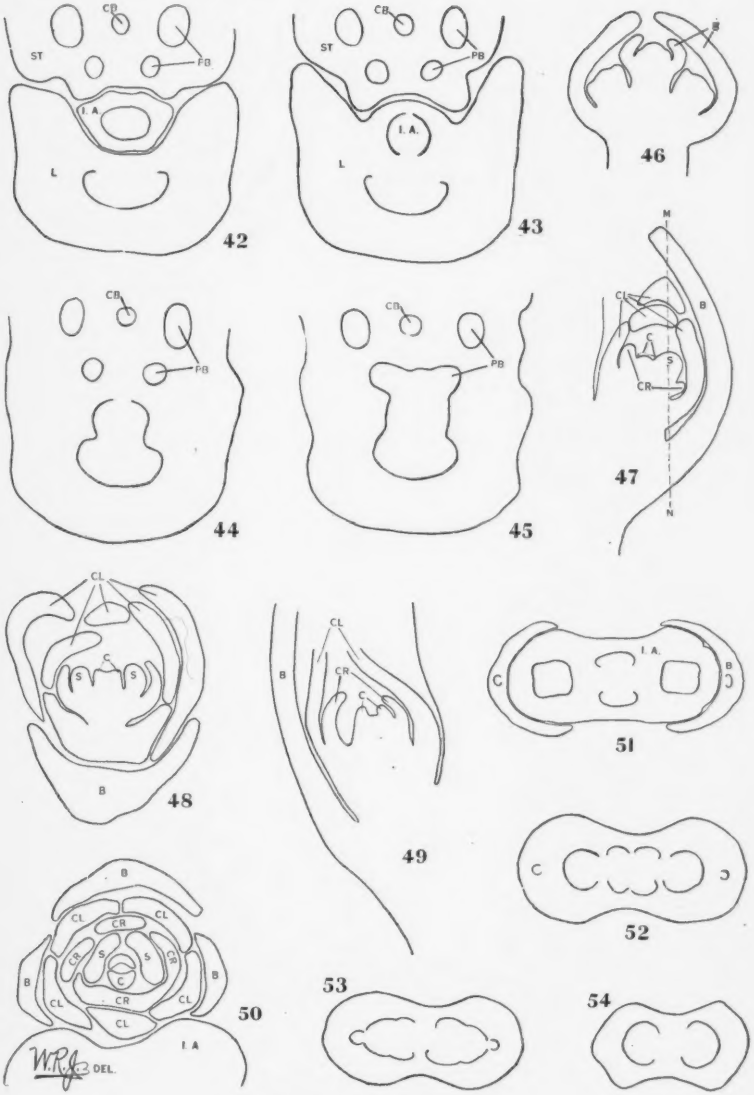

JONES on DIANTHERA

THE TOXIC ACTION OF ORGANIC COMPOUNDS AS MODIFIED BY FERTILIZER SALTS[1]

OSWALD SCHREINER AND J. J. SKINNER

(WITH FIVE FIGURES)

In a former paper[2] the results obtained with dihydroxystearic acid, a crystalline organic compound isolated from a number of unproductive soils, was presented. The results obtained with this organic soil constituent, showing its effect on growth and absorption of plant nutrients from the various culture solutions containing a wide range of fertilizer composition, showed the desirability of obtaining further information concerning the behavior of other organic bodies known to be harmful to plants.

In the present paper some of the results obtained in experiments with toxic organic substances and the restraining influence on their toxicity by fertilizer mixtures of different composition will be given. The compounds studied, though not actually isolated from soil, are common constituents of plant débris, or result from this through changes, and so become, at least temporarily, components of the soil. The effects of a large number of such compounds on plant growth was given in an earlier paper.[3] Of these compounds, cumarin was selected for the continuation of these researches because it was quite harmful even in minute amounts, a few parts per million of solution having a noticeable effect on plant growth, and because it was a common constituent of a number of plants the remains of which get into the soil.

The earlier results were obtained in solutions of the cumarin in distilled water. The present investigation concerns itself with the effect of cumarin in the presence of nutrient salts as well, the

[1] Published by permission of the Secretary of Agriculture, from the Laboratory of Fertility Investigations.

[2] SCHREINER, O., and SKINNER, J. J., Some effects of a harmful organic soil constituent. BOT. GAZ. **50**:161. 1910.

[3] SCHREINER, O., and REED, H. S., The toxic action of certain organic plant constituents. BOT. GAZ. **45**:73, 271. 1908.

essential constituents of these being present to the extent of 80 ppm., but the composition varies. The number of culture solutions of the fertilizer salts used was 66, this being the number requisite to obtain every possible ratio of P_2O_5, NH_3, and K_2O, in 10 per cent stages. The system employed, as well as all details of preparation, was the same as already described in the similar investigation with dihydroxystearic acid already mentioned.

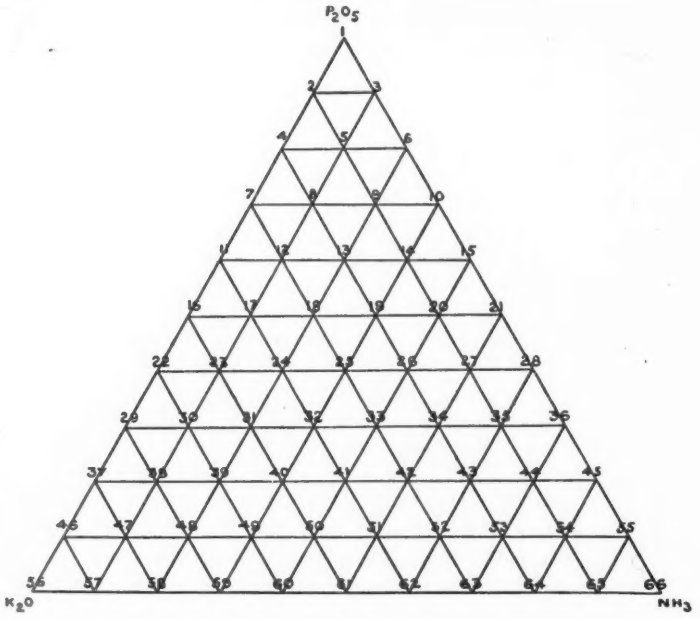

FIG. 1.—Showing the triangular diagram, with the points numbered, which represent the 66 culture solutions.

The triangular diagram is used as a guide. In this diagram (fig. 1), the apices, nos. 1, 56, and 66, are the cultures which contain only the single salts, calcium acid phosphate, sodium nitrate, and potassium sulphate, respectively; that is, the total of 80 ppm. contains 100 per cent of P_2O_5, NH_3, or K_2O, respectively. The line of cultures between 1 and 66 contains mixtures of P_2O_5 and NH_3 in 10 per cent differences; the line of cultures between 1 and 56

contains mixtures of P_2O_5 and K_2O in 10 per cent differences; the line of cultures between 56 and 66 contains mixtures of K_2O and NH_3. The cultures in the interior of the triangle contain mixtures of all constituents, differing in 10 per cent stages one from the other, the composition depending upon its position in the triangle; those nearer the P_2O_5 apex consisting chiefly of phosphate fertilizer, those nearer the NH_3 apex chiefly of nitrate fertilizer, and those nearer to the K_2O apex chiefly of potash fertilizer. For a more detailed explanation of the scheme and principles involved, the reader is referred to an earlier paper.[4]

Two sets of these 66 culture solutions were prepared, one of them containing in every culture 10 ppm. of cumarin. The total concentration of the nutrient elements $P_2O_5+NH_3+K_2O$ was in all cases 80 ppm. The culture solutions were contained in wide-mouth bottles and 10 wheat seedlings grown in each culture after the manner described in the paper cited. The culture solutions were changed every three days, four such changes being made in each experiment. The culture solutions were analyzed immediately after each change for nitrates, but the phosphate and potassium were determined on a composite of the four changes. The green weight of the plants was determined at the termination of the experiment. The first experiment with cumarin was set up on December 9 and discontinued December 21.

The effect of even so low a concentration as 10 ppm. of cumarin was strikingly noticeable in the difference between the plants growing in the two sets of cultures. The appearance of plants growing in solutions containing cumarin is very characteristic and totally different from the effect on wheat of any other toxic compound worked with in this laboratory. The leaves are shorter and broader than is normal for wheat, and only the first leaves are usually unfolded, the other leaves remaining wholly or partially within the swollen sheath; such leaves as do break forth are usually distorted and curled or twisted. The appearance is so characteristic that the investigator can pick out the cumarin-affected plants from those affected by any other toxic body in the same experiment by

[4] SCHREINER, O., and SKINNER, J. J., Ratio of phosphate, nitrate, and potassium on absorption and growth. BOT. GAZ. **50**:1. 1910.

a mere glance. This characteristic behavior of cumarin-affected plants becomes, therefore, in addition to the usual criteria, an indicator of the degree of its harmfulness in the cultures of different composition in this experiment. In addition to its effect on the tops, as just described, there was a general inhibition of root growth, as is the case with many other substances, notably the dihydroxystearic acid already described.

The effect of the cumarin was to depress the green weight of the plants from 100 to 88 as an average in this experiment, although it was obvious from the appearance of the cultures that its effect was far from uniform in all of the cultures, and this is the most interesting feature of the experiment.

It will be recalled that with dihydroxystearic acid the more normal growth was observed in the nitrogen end of the triangle, but when the cumarin cultures were set out in this triangular form according to the composition of the culture solutions, it became at once apparent that the result with the cumarin was not in harmony with the observation so repeatedly made with the dihydroxystearic acid. It was clear that the cumarin had an entirely different effect in the different culture solutions from that observed in the case of dihydroxystearic acid, which had responded most in the fertilizer combinations high in nitrate. With the cumarin the growth was more nearly normal in the fertilizer combinations high in phosphate. In comparing the cultures, those of like composition only are compared in the cumarin and in the normal sets.

This influence of the phosphate on the harmful effect of the cumarin is perhaps most strikingly shown in the difference between the plants growing in the culture solution containing no phosphate whatever, namely along the line 56 to 66 in fig. 1, and the line of cultures immediately above this, containing 10 per cent phosphate in the fertilizer mixture. Where phosphate is entirely absent, the effect of the cumarin is most marked. Above this line the harmful effect of the cumarin steadily decreases, and in the upper part of the triangle disappears altogether, so far as the eye can detect this in the appearance of the plants in the normal and cumarin set.

The effect of the phosphate in overcoming the harmful action

of the cumarin is shown in the green weight of the plants taken at the termination of the experiment. In table I is given the green weight of the series of cultures containing the same amount of phosphate; that is, the series along any one of the horizontal lines in fig. 1.

TABLE I

SHOWING THE INFLUENCE OF PHOSPHATE IN OVERCOMING THE HARMFUL EFFECT OF CUMARIN

PERCENTAGE OF P_2O_5 IN FERTILIZER MIXTURES	PARTS PER MILLION OF P_2O_5 IN ORIGINAL SOLUTIONS	NUMBER OF CULTURES INCLUDED	GREEN WEIGHT OF CULTURES		
			Without cumarin	With cumarin	Relative (without cumarin = 100)
0	0	11	21.773	15.370	70
10	8	10	22.408	18.835	84
20	16	9	20.339	17.140	84
30	24	8	17.143	15.350	90
40	32	7	15.008	14.085	94
50	40	6	11.188	11.150	100
60	48	5	9.113	9.005	99
70	56	4	6.915	6.485	94
80	64	3	4.171	4.330	104
90	72	2	2.388	2.530	106
100	80	1	0.932	0.955	102

The last column of the table gives the relative growth between the two sets of cultures, with and without cumarin. It will be seen from the last column of the table that in those cultures in which no phosphate was present the depression in growth caused by cumarin was greatest, being reduced to 70 per cent of the normal, and that the introduction of 8 ppm. of phosphate caused the growth to rise to 84 per cent of the normal. On further increasing the phosphate content to 16, 24, 32, and 40 ppm., the green weight rose to 84, 90, 94, and 100 per cent of the normal, respectively. From this point on the growth is practically as good in the cumarin set as in the normal control set, thus showing that, on the whole, the fertilizer combinations high in phosphate were practically able to overcome the harmful influence of the toxic cumarin.

The lessened toxicity of cumarin in solutions high in phosphate is also shown when the results of the experiment are grouped in such a way as to obtain all cultures containing 50 per cent and over of any one of the three constituents, P_2O_5, NH_3, and K_2O, as was

done in the case of the dihydroxystearic acid experiment. This is accomplished by taking the cultures contained in the smaller triangles formed at each angle of the larger one shown in fig. 1; that is, the cultures contained within the triangles 1, 16, 21; 21, 61, 66; and 16, 56, 61, respectively. The sum of the green weights in these respective triangles is shown in fig. 2 for the normal and the cumarin sets, together with the relative growth. The phosphate

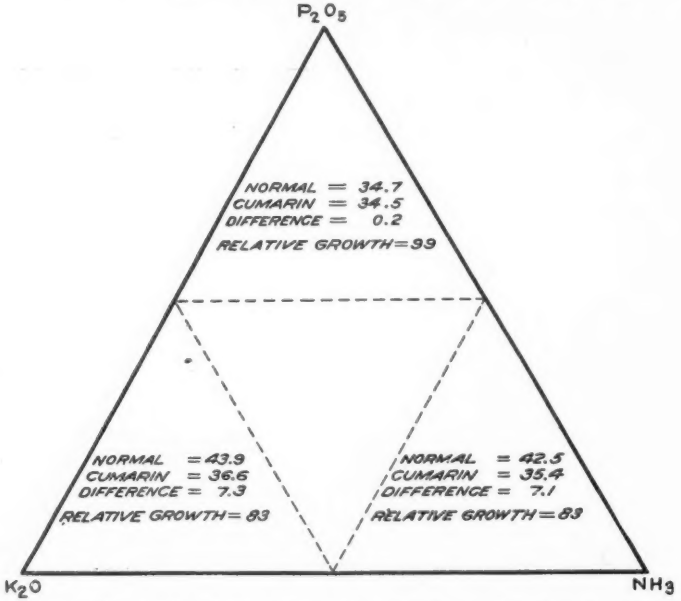

FIG. 2.—Showing the relative growth of normal and cumarin cultures in solutions high in phosphate, nitrate, or potash, respectively.

end shows that the growth in the cumarin set was nearly normal 99 per cent, whereas the potash and the nitrogen end showed a growth only 83 per cent of the normal.

A second set of experiments with cumarin was made and was in all respects conducted as in the first experiment. This grew from January 12 to January 24.

The cumarin-affected plants showed the same characteristic stunting of the leaves as in the former experiment, and, moreover,

again showed strikingly the influence of phosphate in overcoming this effect, the general appearance of the entire triangle of cultures being similar to that already described. The effect of the cumarin was to depress the green weight from 100 to 75 in this second experiment, this being the average depression for all the cultures in the set. Here, as in the first experiment, the toxicity of the cumarin was lessened most in the solutions high in phosphate, being 85 per cent of the normal as compared with 74 and 70 per cent in the cultures high in nitrate and potash, respectively.

The line of cultures containing no phosphate whatsoever again showed the greatest effect of the cumarin; this harmful influence becoming less and less until complete recovery of the plants is noticed in the cultures containing higher amounts of phosphate. The total absence of phosphate showed a depressed growth equal to 62 per cent of the normal; this rises to 70 per cent on the addition of 8 ppm., and to 76 per cent on the addition of 16 ppm., and so on upward, somewhat irregularly but definitely, until in the higher concentration of phosphate the effect of the cumarin is lost entirely.

The foregoing experiments show clearly the influence of cumarin on growth and the effect of phosphate in counteracting the harmful influence of the cumarin. There remains to be considered the influence of the cumarin on the concentration of the solution during the growth of the plant.

Mention has already been made of the fact that the concentration differences produced by the growth of the plants in the various cultures was determined by making an analysis for nitrate at the termination of every three-day change, and of the phosphate and potassium on a composite of the solutions from the four changes. It is thus possible to compare the results obtained under the so-called normal conditions without the cumarin and under the conditions where 10 ppm. of cumarin were present in the solution. The 36 cultures comprising the fertilizer combinations in which all three fertilizer elements are present were consistently analyzed and these only are here considered.

The amount of total $P_2O_5+NH_3+K_2O$ removed from solution by the growing plants in the total number of 36 cultures was 1379 milligrams under the normal conditions and 1272 milligrams in

the cumarin set. In table II are given the results for the P_2O_5, NH_3, and K_2O, separately, under the normal conditions and in the cumarin set.

TABLE II

TOTAL MILLIGRAMS OF P_2O_5, NH_3, AND K_2O REMOVED FROM THE 36 CULTURE SOLUTIONS CONTAINING ALL THREE OF THESE INGREDIENTS

	TOTAL ABSORPTION IN MILLIGRAMS		RELATIVE	PERCENTAGE OF CUMARIN CULTURES ABOVE NORMAL
	Normal	Cumarin		
P_2O_5	278.5	264.5	95	57
NH_3	482.6	415.3	86	22
K_2O	618.2	592.6	96	39

An examination of these figures discloses the fact at once that while the cumarin has decreased the absorption of these nutrient elements, it has not decreased it anywhere near the extent shown by dihydroxystearic acid in the experiment cited. The third column of figures gives the relative effect of cumarin absorption of each nutrient element, and indicates that the phosphate and potash absorptions were the more nearly normal of the three, especially the phosphate absorption if the figures in the last column are taken into account. This column gives the percentages of the individual cumarin cultures which showed an absorption equal to or greater than the corresponding culture without cumarin.

In the second experiment this effect is clearly marked, the phosphate absorption being 91 per cent of the normal, as compared with 78 and 87 for the nitrate and potash, respectively. In this experiment the total absorption of $P_2O_5+NH_3+K_2O$ was 1267 milligrams under normal conditions and 1077 milligrams with cumarin.

While these figures indicate a somewhat more normal phosphate absorption in the cumarin set than normal nitrate or normal potash absorption, the figures are, nevertheless, not decisive enough to enable one to say definitely that the antagonism of the phosphate to cumarin, as shown in the growth of the plants, is due to this cause alone. A rigid examination of the complete data does not allow us to draw this conclusion without at the same time suggesting the possibility of an external interaction between the lactone

cumarin and the acid calcium phosphate. The possible solutions of the problem must be left for future investigation.

From the foregoing results it is apparent that the two toxic substances studied, dihydroxystearic acid and cumarin, show markedly different physiological properties, and are very differently influenced by fertilizer salts. Whether this is a direct action of the fertilizer on the organic body or through the medium of the plant cells, making the toxic substance and the particular fertilizer salt physiologically antagonistic, cannot be definitely stated.

The cumarin so affected the normal development of the wheat as to cause stunting of leaf growth, with abnormal appearance associated with a slightly altered absorption of plant nutrients, both as to amount and ratio, the phosphate absorption being the more normal. The fertilizer combinations high in phosphate were the most effective in antagonizing the harmful effect of cumarin.

The dihydroxystearic acid also affected normal development, causing a decrease in top growth, but no abnormal appearance, the greatest abnormality being in this case observed in the root system, which was darkened and much stunted and showed swollen root tips, often bending into fishhooks, associated with a much altered absorption of nutrient elements both as to amount and ratio, the phosphate and potassium absorption being greatly depressed, the nitrate removal or disappearance being about as under normal conditions, but relatively much greater. The fertilizer combinations high in nitrate were the most effective in overcoming the harmful effect of this soil constituent.

In view of this widely different behavior of these two toxic substances, entailing the interesting observation that they responded differently to the different fertilizer combinations, it was thought desirable to consider some results with other toxic substances. In the first place, it was interesting to see whether the result observed with dihydroxystearic acid, namely response to the nitrate, was shown by another toxic body, and thus throw a little more light on this phase of the question. For this comparison the aldehyde vanillin was selected. This was known to be toxic from former experiments, was known to be oxidized by the plant roots, and was further known to be more readily oxidized when nitrates

were present,[5] and so should be a body which would behave much like dihydroxystearic acid.

In the present experiment with vanillin here recorded, the same number of cultures (66), containing all the fertilizer combinations possible in 10 per cent stages, was used as in the experiment with the dihydroxystearic acid and cumarin. The concentration of vanillin used was 50 ppm. The duration of the experiment was from March 7 to March 19. The solutions were changed every three days as in the cumarin experiment already described, but no analyses of the solutions were made in this case. The green weight, however, was recorded.

The effect of the vanillin was not so marked on the tops as on the roots, although in the regions of better growth this also was not very prominent. The general appearance of the plants resembles the effect produced by dihydroxystearic acid much more than the effect produced by cumarin under the same circumstances. The region of greatest growth appeared also, as in the case of dihydroxystearic acid, to be shifted toward the nitrogen end of the triangle. The plant growth was 84 per cent of the normal as an average of all the cultures.

For the present purpose, however, the growth in the cultures respectively high in phosphate, nitrate, or potash is of paramount interest. This grouping of the results obtained on the green weights at the termination of the experiment is shown in fig. 3. The relative growth in the cultures having 50 per cent and more of phosphate was 85 per cent of the growth without the vanillin; for the cultures mainly nitrogenous it was 88; and for the cultures mainly potassic it was 82. It will be observed that the vanillin depressed the growth least in the cultures high in nitrate, a result in harmony with previous observations on the toxicity of vanillin and in harmony with the action of dihydroxystearic acid. Both of these substances have reducing properties; that is, they are themselves readily oxidized; both have an inhibiting effect on root oxidation and on root growth generally; both are overcome by the fertilizer combinations which increase root oxidation to the greatest extent. It was consequently thought to be of interest to

[5] SCHREINER and REED, Jour. Amer. Chem. Soc. **30**:85. 1908.

see what the effect of an organic compound having oxidizing properties would be on plants growing in these various fertilizer combinations. For this purpose quinone, shown to be toxic to wheat seedlings in a former research, was chosen, inasmuch as it is an oxidizing substance and therefore in strong contrast to the vanillin with its decided reducing properties. This fundamental difference

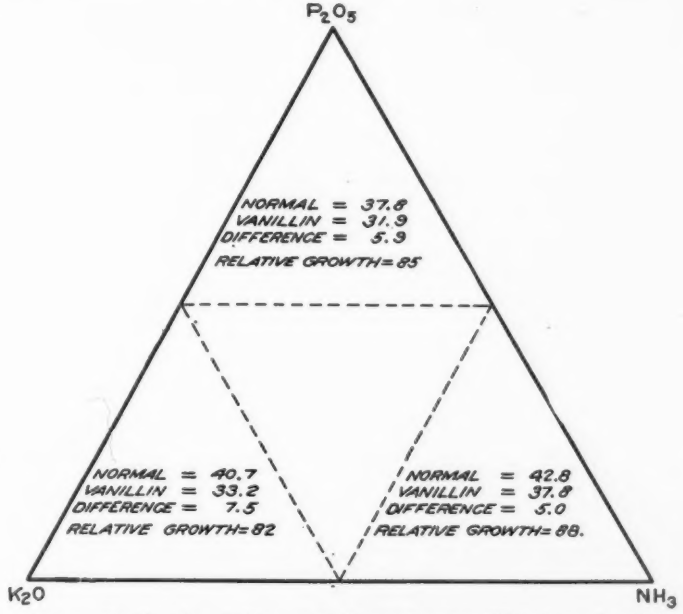

FIG. 3.—Showing the relative growth of normal and vanillin cultures in solutions high in phosphate, nitrate, or potash, respectively.

in the properties of the two compounds, it was thought, should show itself in an altered metabolism of the plants under the influence of two such widely different poisons, and the scope of the present experiment as to different fertilizer combinations should lend itself to showing such differences in metabolism or fertilizer requirement, and thus throw some light upon the behavior of crops in the field toward fertilizers under oxidizing conditions.

In the experiments with quinone the fertilizer combinations and

general technique were the same as in the preceding experiments with vanillin and cumarin, the concentration of quinone being 10 ppm. No analyses of the solutions were made in this experiment. The duration of the experiment was from March 23 to April 4.

The effect of the quinone on the development of the wheat was in itself as definite, though perhaps not as characteristic, as the effect of cumarin. The effect of the latter substance was to produce short, broad, irregularly developed leaves and stunted tops; the effect of the quinone was to produce long, thin leaves, producing tall, slender plants, so that at first glance the quinone in the concentration here used appeared to have had little effect on the growth of the plants. Closer inspection, however, shows the plants to be slender and weaker, although the leaves may be fully as long as the normal leaves. The effect of quinone on plant growth, however, is definitely shown by the decreased green weight. The root growth is also affected.

The most interesting feature of difference between the normal and quinone sets of cultures, observable when both sets are arranged in triangular form according to the composition of the culture solution, is the apparent or real shifting of the greater growth toward the potassium end of the triangle in the quinone set, accompanied by a generally better relative growth in the potash angle. This observation would seem to show that the quinone effect was counterbalanced by the fertilizer combinations high in potash, whereas cumarin was undoubtedly affected by the phosphate fertilizers, as shown, and vanillin as well as dihydroxystearic acid by the mainly nitrogenous fertilizers. This effect was not anticipated, but might easily have been, inasmuch as quinone is a strong oxidizing substance and potash salts are known from a previous research[6] to be retarders of root oxidation, analogous to the opposite effect of vanillin, a reducing substance overcome by nitrate known to stimulate root oxidation.

The green weights obtained at the end of the experiment bear out this observation. The relative growth in the quinone set was 75 per cent of the normal. The chief interest, however, centers

[6] SCHREINER, O., and REED, H. S., The rôle of oxidation in soil fertility. Bull. 56, Bureau of Soils, U.S. Dept. Agr. 1909.

in the comparative results obtained in the cultures containing 50 per cent and more of the phosphate, nitrate, and potash, respectively, in order to see which of these was the most efficient in antagonizing the action of quinone. The results of the grouping of cultures on this basis, made as explained in the preceding experiment, is shown in fig. 4. The mainly phosphatic fertilizer combinations show a relative green weight of 77 per cent of the normal,

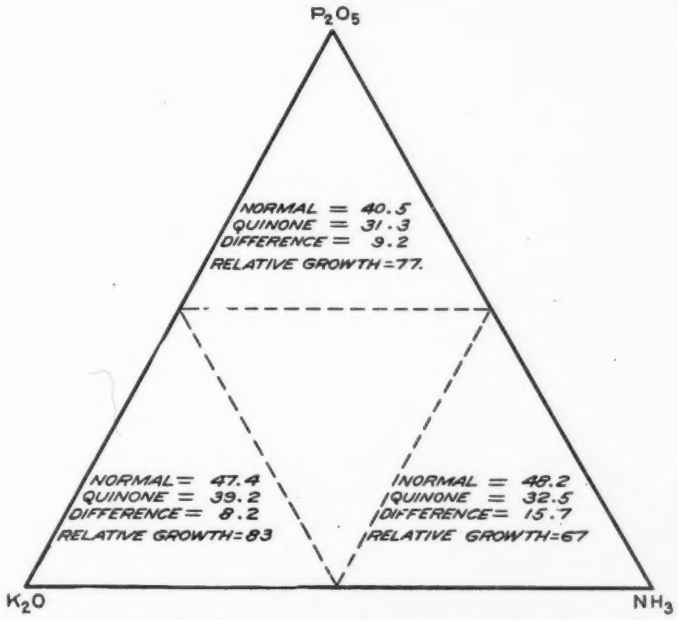

FIG. 4.—Showing the relative growth of normal and quinone cultures in solutions high in phosphate, nitrate, or potash, respectively.

the mainly nitrogenous 67, and the mainly potassic 83. It is observed that the potash fertilizers were the most efficient in overcoming the harmful effect of quinone.

This experiment with quinone was repeated, and this time the solutions were analyzed as in the case of the cumarin experiment. This second quinone experiment lasted from April 8 to April 20. It showed the same general slender appearance of the plants, as

well as again showing the influence of the potassium fertilizers as above described. In this experiment the green weight in the quinone set as a whole was 79 per cent of that in the normal. The results for the mainly phosphatic, mainly nitrogenous, and mainly potassic fertilizers are 76, 77, and 85, respectively, again showing the relative greater efficiency of the potash fertilizers in this quinone experiment.

These quinone experiments indicate clearly the harmful influence of quinone on growth, and the effect of potassium in counteracting this action of the quinone. In the second experiment the cultures were analyzed for phosphate, nitrate, and potassium, and it is, therefore, interesting to inspect these data, as was done with the cumarin results. Only the 36 cultures having the combinations of all three fertilizer salts are considered.

The amount of total $P_2O_5+NH_3+K_2O$ removed from solution by the growing plants in the total number of 36 cultures was 1568 milligrams in the normal set and 1327 milligrams in the quinone set, showing a decrease in the sum total of P_2O_5, NH_3, and K_2O removed when quinone is present. In table III are given the results for the P_2O_5, NH_3, and K_2O separately under the normal conditions and in the quinone set.

TABLE III

TOTAL MILLIGRAMS OF P_2O_5, NH_3, AND K_2O REMOVED FROM THE 36 CULTURE SOLUTIONS CONTAINING ALL THREE OF THESE INGREDIENTS

	TOTAL ABSORPTION IN MILLIGRAMS		RELATIVE	PERCENTAGE OF QUINONE CULTURES ABOVE NORMAL
	Normal	Quinone		
P_2O_5	300.4	173.6	58	8
NH_3	571.5	506.8	89	11
K_2O	696.5	646.5	93	36

An inspection of these figures indicates strongly that the potassium absorption in the presence of quinone has been more normal than the other two nutrient elements. This is shown both by the relative absorption in the third column and by the number of quinone cultures showing normal or greater absorption of P_2O_5, NH_3, and K_2O, respectively, in the last column.

We have, therefore, the interesting case of a toxic oxidizing body being overcome by a fertilizer salt having a restraining action on the normal oxidative power of the root, accompanied by a relatively greater absorption of this fertilizer element than under normal conditions.

Discussion and summary

In the foregoing experiments with cumarin, vanillin, and quinone, the effects of these toxic substances on the development of wheat seedlings was demonstrable by three criteria:

1. By decreased green weight.

2. By the morphological effects as shown by their general appearance. Cumarin-affected plants have characteristic stunted tops, broad, distorted leaves; vanillin-affected plants are less characteristic, but show decreased growth of top and strongly inhibited root growth; quinone-affected plants are tall and slender, with thin, narrow leaves, in strong contrast to the cumarin-affected plants. The substances show, therefore, a markedly different behavior in detail, although all show a toxic effect in inhibiting growth.

3. By decreased absorption of plant nutrients. The cumarin depressed potash and nitrate removal from nutrient solution more than phosphate; the quinone, on the other hand, depressed phosphate and nitrate more than potash; the effect of vanillin was not determined in this regard. It might be interesting to mention, however, that dihydroxystearic acid, which appears to act much as vanillin did, depressed phosphate, and potash more than nitrate. In this respect again the influence of the various harmful substances was different.

The various fertilizer salts acted differently in overcoming the respective harmful effects of these toxic compounds. The mainly phosphatic fertilizers were the most efficient in overcoming the cumarin effects; the mainly nitrogenous fertilizers in overcoming the vanillin effects; the mainly potassic in overcoming the quinone effects.

This different action of fertilizer salts on the toxic compounds is also illustrated by the diagrammatic representations in fig. 5 of the regions of greatest growth obtained in the various

experiments. The triangle represents the various cultures containing the fertilizer combinations, as is fully explained in fig. 1 and the accompanying text.

Under normal conditions, that is, without any toxic body present, the greatest growth is found in those cultures low in phosphate and about halfway between the nitrate and potash angles. This

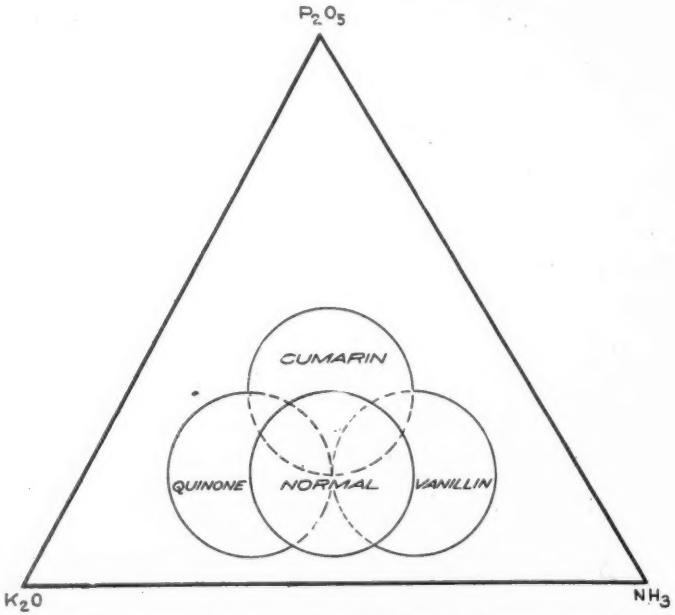

FIG. 5.—Diagrammatic representation of the region of greatest growth in the triangle culture experiments with cumarin, vanillin, and quinone.

region of greatest growth is diagrammatically represented by the circle marked normal in fig. 5. When cumarin is present in the cultures, the effect was to cause the region of greatest growth to shift in the direction of the phosphate angle, a condition which may be diagrammatically shown by the circle marked cumarin. With quinone, this region of growth was shifted toward the potash angle, and with vanillin toward the nitrate angle, as illustrated in the diagram.

This shifting of the region of greatest growth was accompanied by a corresponding change in the absorption of plant nutrients, although this is not as marked as the green weight. All of these facts are in harmony with the conclusion drawn from the data already given, that phosphate fertilizers were antagonistic to cumarin, that potash fertilizers were antagonistic to quinone, and that nitrate fertilizers were antagonistic to vanillin and to dihydroxystearic acid.

In regard to the exact mechanism of the chemical or physiological character of the interactions between these toxic substances and the fertilizer salts, nothing definite can be said. Attention, however, should be called in this connection to the fact that the reducing poisons vanillin and dihydroxystearic acid are antagonized by those fertilizer combinations which stimulate oxidation, and that the oxidizing poison quinone is antagonized by the fertilizer combinations checking oxidation, thus indicating that there is some correlation between these functions. A discussion of the interaction of cumarin and phosphate fertilizers would be mere speculation in the present state of our knowledge.

Attention must also be called again to the fact that the observations here recorded for phosphate, nitrate, and potash were obtained with the salts, calcium acid phosphate, sodium nitrate, and potassium sulphate, and that the observed results, therefore, may be caused by these substances as a whole, that is, as combinations rather than individual elements. For deciding this question, further investigation is necessary, involving experiments with other salts and combinations.

These actions of the different fertilizer combinations or different fertilizer requirements, as they may be styled, show a certain parallelism with field observations on soils and their fertilizer requirements, and one is tempted to ask to what extent may the different fertilizer requirements of different soils or of the same soil under different conditions be influenced by the same cause. That harmful bodies occur in soils has been amply shown, and that these are influenced directly or indirectly by fertilizer salts is also clear from this and other researches. That the constitution of the organic matter varies from soil to soil, and in the same soil under

different conditions of aeration, drainage, and cropping, is likewise clear. The presence of compounds inimical to plant growth by virtue of a property resembling that of any of the above-mentioned poisons might therefore cause a different fertilizer requirement, a requirement which might even change from time to time according to the nature of the biochemical reactions producing the body, or according to the nature of the plant remains in the soil; in other words, according to rotation, with its necessary altered soil management, and the altered biochemical changes produced in the different plant remains.

The action of fertilizers on soils is a much contested question, but the weight of evidence is against the assumption that their effect is due altogether to the added plant food. If so simple an explanation were the true one, nearly a century of investigation of this problem by scientists of all civilized nations would surely have produced greater unanimity of opinion than now exists in regard to fertilization. Thoughtful investigators everywhere are finding that fertilizer salts are influencing many factors which contribute toward plant production besides the direct nutrient factor for the plant. It is this additional influence of fertilizers which makes them doubly effective when rightly used and inefficient when improperly used. To this influence of fertilizers on soil and biological conditions is due their capriciousness when applied on the theory of lacking plant food, and any study which throws further light upon the mooted question is of direct help toward reaching that view of soil fertility and soil fertilization which will eventually result in a more definite system of fertilizer practice, to the end that surer and safer returns are obtained from their use. This will tend to extend fertilizer practice by making it more remunerative and rational than in the past.

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THE EFFECT OF EXTERNAL CONDITIONS UPON THE AFTER-RIPENING OF THE SEEDS OF CRATAEGUS MOLLIS

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It is well known that the seeds of many plants do not germinate immediately after ripening, but only after a period of rest which in some cases no doubt extends into years. NOBBE and HANLEIN (16), for example, kept certain weed seeds under germinating conditions for a period of 1173 days without germination.

While various workers have done much in the way of adding to the list of seeds that require a rest period before germination, little has been done to determine the real cause of this delay or dormancy on the part of the seed. During this period, it is assumed that the seed undergoes certain changes, at the completion of which germination may take place. This period of preparation for germination has been termed the after-ripening period. The term after-ripening then may be made to include the necessary protoplasmic changes antecedent to germination; changes involving the release of digestive and respiratory enzymes, thus leading to rapid metabolism; or disintegration or other modifications of incasing structures that limit the water or oxygen supply or even mechanically hinder growth. But in relatively few cases do we know to which of these dormancy is due. In most literature the cause is assumed to be the need of protoplasmic changes in the embryo. In this paper we have used the term after-ripening in reference to embryonic changes whether protoplasmic or metabolic, in contrast to those changes that merely affect the incasing structures. By germination we mean the growth of the hypocotyl.

Many more or less successful attempts have been made to shorten or eliminate altogether this period of inactivity on the part of the embryo by certain stimuli designed to arouse the dormant protoplasm to activity. Lately FISCHER (5) observed that seeds of certain water plants might be kept in water free from fermentation

for years without germination, but if fermentation were set up, the seeds would soon after begin to germinate. He attributed this to the effect of H+ or OH− ions acting as stimuli on the dormant protoplasm. MÜLLER (**15**) found that the seeds of *Eichhornia* and *Heteranthera* germinate only after desiccation. CROCKER (**1**), working on the seeds of various water plants, including *Eichhornia* and others reported by FISCHER, has shown that the protoplasm is not dormant. He found that the seeds of *Eichhornia*, *Alisma Plantago*, and *Sagittaria* germinate readily in distilled water if the coats were broken, and concluded that bases and acids here must have their effect upon the seed coats rather than upon the embryos. He also concluded that the effect of the coats in many of the seeds of water plants is mainly to limit the water rather than oxygen supply, since little if any oxygen is needed by them for germination.

KINZEL (**11**) and HEINRICHER (**8**) have shown that in many seeds light is necessary for germination. Seeds kept under ordinary germinating conditions for months in darkness failed to germinate, but when placed in light germinate within a few days. Both KINZEL and HEINRICHER seem to have taken it for granted that the changes induced by the light have to do with the embryo. But even here it is barely possible that light in some way affected the seed coat, rendering it permeable.

It has long been known that cold has an influence in some way on the germination of various seeds. Many seeds are thought to germinate only after being subjected to freezing and thawing. But as to the exact effect of the cold in bringing about germination there is as yet nothing very definite.

PAMMEL and LUMMIS (**17**) found that many weed seeds that failed to germinate under ordinary germinating conditions germinated more or less readily after freezing. PAMMEL and KING (**18**) have shown that freezing and thawing not only increase the percentage of germination in many weed seeds, but that the seeds thus treated in many cases germinate more quickly than those kept dry before planting. FAWCETT (**4**) likewise has shown that freezing and thawing shortens the dormant period of many weed seeds, and that the percentage of germination of seeds exposed to

the weather is in many cases considerably higher than of those kept dry. In wild rye, for instance, the dormant period was reduced from 9 to 5 days, and the percentage of germination was raised from 2 to 48. But the limiting factors to growth have not been located in any of these cases.

Investigation

This work on the germination of the seeds of the hawthorn (*Crataegus mollis*) was undertaken in order to determine so far as possible the influence of the various external conditions affecting their after-ripening. Hawthorn seeds usually do not germinate until the second or even third year after the fruit has ripened. KUNTZE (**14**) wrote in 1881: "Hawthorn berries (*Crataegus*) which do not germinate until the second year are peculiarly treated. They are mixed with sand, thrown into a heap, and watered a few times in a cold house during the winter, and sown the following spring. They are turned over several times so that the pulp may decompose." The *Cyclopedia of American horticulture* (**3**) also refers to this delay in the germination of the seeds of the hawthorn and gives the method employed in their germination essentially as that given by KUNTZE.

In considering the after-ripening and germination of the hawthorn, the various structures about the seed, as the pericarp and carpels, as well as the testa and embryo itself, must not be overlooked. The pericarp is separated from the carpels by decay or by being eaten off by some animal. It often shrivels and remains intact for a considerable length of time. The carpels are bony and the seed is freed only after much weathering, when the carpels become more or less porous to water and are split by the swelling of the seeds. Both of these structures in nature, by the prevention of a sufficient supply of water and oxygen, may tend to prolong after-ripening as well as delay germination.

Our first work was to determine the behavior of the seeds under ordinary germinating conditions. To do this we removed the pulp and the bony carpel. The seeds were than placed upon wet cotton in Petri dishes, both in the laboratory and the greenhouse. They remained in this condition for months without any sign of germina-

tion, and all those seeds that had suffered injury, however slight, in removing them from the carpels invariably decayed.

To remove the possibility of coat effects, we next removed the testas and treated the embryos as above; when thus treated an occasional hypocotyl grew, varying from none to 3 or 4 per cent. CROCKER (**2**), who previously employed this method, indicated a higher percentage of growth. The behavior of the embryos under these conditions as pointed out by him is interesting in that it shows a remarkable correlation between the cotyledons and the hypocotyl. In the light the cotyledons soon turn a dark green and enlarge often to several times their original size. The hypocotyl does not elongate, but remains short and blunt. In case of germination after complete after-ripening, the hypocotyl takes precedence and elongates rapidly, while the cotyledons increase in size much more slowly and never reach the size attained in case the hypocotyl fails to elongate. In darkness the behavior was similar, except that the cotyledons contained xanthophyll.

We next carried on experiments to determine the effect of low temperatures in bringing about after-ripening and germination. The first set of experiments was carried on in an ordinary ice chest so arranged as to admit light to some of the cultures. With this we were able to obtain a temperature of 5°–6° C.

In all cases the seeds treated were placed on wet cotton in Petri dishes or in air-tight jars, excepting those seeds that were subjected to low temperatures in a dry state or under water. These were treated in test tubes with cotton plugs. Table I gives the results of the first set of experiments.

In these cultures the number of seeds germinated compared with the total number treated may seem rather low, varying as they do from 50 to 80 per cent. This is not due to the seeds failing to germinate when removed from the cold, but almost entirely to loss during the process of after-ripening. It is quite difficult to remove the seeds from the carpels without injuring them. While in all cases they were removed by carefully splitting the carpels with the point of a strong knife, yet many suffered more or less injury that escaped observation until placed upon the ice. The seeds with their testas broken invariably decayed during the pro-

cess. Seeds with the testas broken decay more readily than those with the testas removed, because the edges of the broken testas offer a good lodging-place for bacteria and the spores of various fungi. The seeds during the after-ripening process require considerable care. They should be removed occasionally, washed, sorted, and placed upon clean wet cotton. They are especially liable to decay if they are left in a mass. The loss in after-ripening can be greatly reduced by thoroughly washing the seeds before placing them in the cold.

TABLE I

No. culture	No. seeds	Condition of seeds under treatment	Temperature	No. days at low temperature	In light	In dark	Germination within 10 days	Total number germinated after 20 days
14....	400	Carpels off.....	5–6°	96	—		221	264
13....	400	Carpels on.....	5–6°	242	—		0	0
18....	400	Carpels off.....	5–6°	96		—	122	250
17....	400	Carpels on.....	5–6°	242		—	0	0
9....	400	Carpels off.....	5–6°	96		—	5	219
8....	400	Carpels off.....	5–6°	96		—	244	311
16....	400	Carpels off (seeds dry)..	5–6°	96		—	0	0
19....	400	Carpels off (seeds under water).....	5–6°	150		—	0	0

Germination at 10°–12° C.

When the seeds had been left a sufficient time in the cold to after-ripen, the percentage of germination based upon the number coming from the cold was always high, running from 90 to 98 per cent.

When the above seeds were removed from the cold and were placed in a water bath at a temperature of 10° to 12° C. to germinate, practically all the seeds, except those treated dry or under water or with carpels on, germinated, but the time required was somewhat extended. In later experiments, where seeds were removed from the cold to the temperature of the greenhouse, the period of germination covered a much shorter time, as will be seen in table II.

The seeds treated under water and those treated dry showed no signs of after-ripening; when they were removed from the cold, they decayed. The failure to after-ripen under water was probably due to an insufficient supply of oxygen. Seeds treated with carpels

on showed considerable progress in after-ripening. During the latter part of the period in the cold there was occasional germination, and when the carpels and coats were removed, the embryos generally responded normally.

TABLE II

No. culture	No. seeds	Temperature	No. days at low temperature	Germination within 5 days	Germination within 10 days	Remarks
1.....	150	5–6	73	109	112	
2.....	150	0	73	45	68	
21.....	150	0	90	82	83	
4.....	150	−2 to −3	75	0	0	
23.....	150	−2 to −3	77	0	0	
24.....	150	−2 to −3	114	0	0	
10.....	150	5–6	130	0	0	Treated without oxygen
20.....	150	5–6	130	0	0	Treated H_2 with 2 per cent oxygen
5.....	150	5–6	90	5	5	Treated without oxygen
3.....	150	0	90	0	0	Treated without oxygen
7.....	150	0	90	0	0	Treated H_2 with 2 per cent oxygen

The above experiments were conducted in an ice chest so constructed that by means of salt three fairly constant temperatures were obtained: 5° to 6°, 0°, and −2° to −3° C. The seeds were freed from the carpels and after-ripened in the dark.

It will be noticed that the time the seeds were left in the cold to after-ripen is in some cases less than that in the previous table, and also that the seeds germinated more quickly when removed from the cold. The seeds were removed from the cold directly to the greenhouse instead of the bath, as in the first set of experiments.

In culture no. 1, 109 seeds responded within 3 days, and the 3 remaining within 5 days. Not more than 2 or 3 seeds decayed after they were removed from the cold. The average length of the hypocotyls after 5 days was 15 mm. In no. 2, the germination was slower, the hypocotyls elongated less rapidly, and many decayed when taken from the cold. No. 21 remained 17 days longer in the cold than no. 2, which no doubt accounts for the greater number germinated. Nos. 4, 23, and 24, although left at the low temperature from 75 to 114 days, showed no signs of germination.

Nos. 10, 20, 5, 3, and 7 were arranged to determine the relation of oxygen to after-ripening. The seeds in these cultures were placed on wet cotton in Novy jars of about a liter capacity. Nos. 10, 5, and 3 were without oxygen. The oxygen in no. 5 was removed by pyrogallate. In nos. 10 and 3 the jars contained hydrogen washed in pyrogallate. No. 20 contained hydrogen washed in KOH and $KMnO_4$. The hydrogen used was from the Linde Air Products Company of Buffalo, N.Y. Upon analysis it was found to contain 2 per cent oxygen. The results with no oxygen or even 2 per cent were mainly negative.

Several cultures were treated with ether in addition to the cold. The seeds were placed in air-tight jars of a liter capacity. In each jar there was a small bottle containing 10 cc. of water, to which had been added ether varying in the different cultures from 0.25 cc. to 1 cc. The jars were then placed in the cold from 8 to 16 days. At the end of this period the seeds were removed from the jars, placed in Petri dishes, and returned to the cold. The germination in every case was less than that of the control culture without ether. While ether may have a stimulating effect upon germinating seeds, the concentrations used here retarded rather than hastened after-ripening.

To determine the effect of a temperature upon after-ripening somewhat higher than the ones previously employed, the following cultures were placed in a water bath December 1 in which the temperature at the beginning was 9°–10° C. Tap water was used in the bath and the temperature varied with the season, ranging from the above temperature to as high as 22° C. in July and August. The seeds were freed from the carpels. Table III shows the results of these experiments. As fast as the seeds were after-ripened and germinated, they were counted and removed from the bath.

All these cultures were put in the water bath December 1, excepting no. −1, which was placed there 10 days later. This gave it 10 days less exposure to the low temperature at the beginning, and this in part, at least, may account for the difference in the number of seeds germinated between it and no. 1. There is also brought out in this table a very marked falling off in germination as the temperature rose, which means, of course, a similar falling

off in the number of seeds after-ripened. Several of the seeds that germinated late in the season had rather stunted hypocotyls. The difference in the number of seeds germinated in the light and the dark at these temperatures seems to indicate that light at least at these temperatures had some influence on the after-ripening.

TABLE III

No.	No. seeds	Carpels		Temp.	No. days in bath	Light	Dark	Germination during						Total
		On	Off					Mar.	Apr.	May	June	July	Aug.	
1..	400		/	9–22° C.	275	/		40	25	15	11	11	1	103
—1..	400		/	9–22° C.	264	/		8	9	12	17	11	3	60
2..	400		/	9–22° C.	275		/	9	1	0	7	1	1	19
3..	400	/		9–22° C.	275	/		5	2	0	0	0	0	7
4..	400	/		9–22° C.	275		/	0	0	0	0	0	0	0

To determine the effect of alternating high and low temperatures, a culture (no. 9) was placed in the above water bath April 13. The temperature of the bath at this time was about 13° C. It was left at this temperature for 10 days, when it was removed to the ice chest at a temperature of about 6° C. This 10-day alternation was kept up until September, or for 140 days. None of the seeds germinated during this time, although they had been exposed one-half of that time, or 70 days, to a temperature most suitable for after-ripening. The high temperatures appear to have counteracted the effect of the low temperatures.

In order to ascertain the importance of the testas in after-ripening, they were removed from 50 seeds and the embryos were placed in the cold at a temperature of about 6° C. At the end of 28 days several of the embryos showed signs of germination. They were then removed from the cold to the greenhouse, and within 10 days 39 of the 50, or 78 per cent of the seeds treated, had germinated. The time required for after-ripening seeds without testas was about one-third of that required for seeds with testas, under conditions otherwise the same.

In the after-ripening of these embryos the correlation between cotyledons and hypocotyl was made very evident. The embryos to after-ripen must be kept at a temperature sufficiently low to inhibit growth in the cotyledons. When the embryos were exposed

but a short time to high temperature, the cotyledons began to enlarge, and if exposed to light to turn green and after-ripening would not take place.

The importance of water as a factor in the after-ripening of the seeds of the hawthorn needs to be emphasized. Those seeds kept thoroughly wet during this process gave the best results, as indicated by the germination when removed from the cold. The prolonged period of after-ripening of seeds within the carpels, the shorter period when the carpels were removed, and the still shorter period when both carpels and testas were removed show that these structures add greatly to the resting period. In order to determine to what extent the carpels and testas interfered with the taking up of water by the embryo, we took two lots of seeds, one with the carpel intact, and the other with carpels removed. Each lot was soaked in water at room temperature for 48 hours. The testas were then removed from a portion of the second lot. These three sets of seeds, one with carpels intact, one with testas, and the other with both carpels and testas removed, were placed upon wet cotton in Petri dishes and left in an ice chest at about 7° C. for 14 days. At the end of this period the carpels and testas were removed from all seeds which had been treated with them on, and the water content of the embryos determined for the three conditions. The embryos were dried in vacuo over H_2SO_4. The determinations were made in duplicate and are given in table IV.

TABLE IV

No. seeds treated	Condition of embryos during treatment	Wet weight of embryos in grams	Dry weight of embryos in grams	Water content in grams	Water content in percentage
42.....	Carpels on..	0.5114	0.3844	0.127	24.8
25.....	Carpels on..	0.3186	0.2396	0.0796	24.9
29.....	Testas on...	0.4018	0.2730	0.1278	32.5
44.....	Testas on...	0.6056	0.4180	0.1876	30.9
44.....	Testas off...	0.6866	0.4100	0.2766	39.4
30.....	Testas off...	0.4810	0.2904	0.1906	39.6

GASSNER (**6**) has shown that seeds of two South American grasses, *Chloris ciliata* and *C. distichophylla*, after-ripen in dry storage. The most favorable period of dry storage was found to be 30–40 weeks. He also found light to be an important factor

in their germination when removed from dry storage, light favoring and darkness hindering germination. After 10 weeks of dry storage, there was no germination in darkness at the optimum temperature, but after 39 weeks, 7–8 per cent germinated under the same conditions. In light after 9 weeks of dry storage, 73 per cent germinated under the same conditions. In a recent article (**7**) covering a study of *Stenotaphrum glabrum* and *Paspalum dilatatum*, GASSNER found that *P. dilatatum* after-ripened in 1 to 2 weeks in dry storage at 50°–60° C.

The after-ripening of these seeds in dry storage is most interesting, especially if it is a true case of after-ripening, that is if the cause of delay lies in the embryo rather than in the coat. If the delay were due to an impermeable coat, it would not be difficult to understand how drying might cause it to rupture or change otherwise its permeability to water or oxygen. The presence of water is usually necessary to initiate chemical changes. This is especially true for germination, and in the hawthorn, at least, is also true for after-ripening, since neither the seeds kept dry for long periods at the temperature of the laboratory nor at temperatures most favorable for after-ripening showed any signs of germination when placed under germinating conditions.

The claim that certain seeds after-ripen in dry storage is quite general. KINZEL (**13**) found that for oats kept in dry storage the percentage of germination increased for 8 months after harvesting and then gradually fell. But in all these cases there is need of a thorough analytical study of the processes involved in the after-ripening.

Some general considerations

The preceding tables indicate that the after-ripening in the hawthorn takes place at low temperatures, the optimum for which is 5° to 6° C. But the process goes on even at 0° C., while at −2° C. to −3° C. it makes little or no progress. Freezing and thawing, then, do not appear to be the ideal conditions for after-ripening. The value of freezing and thawing to seeds which are lying in the soil, in which cold is a factor in the after-ripening, very likely consists in rupturing the seed coat or other external structures, by means of which water or oxygen are permitted to enter. Especially

is this true of seeds in which the cause of the delay is in the external structures rather than in the embryo. In the hawthorn, freezing and thawing undoubtedly bring about a splitting of the bony carpels sooner than would otherwise occur, and in this manner shorten the period of after-ripening.

Temperatures alternating between that most favorable for after-ripening, as 5° to 6° C., and temperatures ranging from 13° to 22° C. were not favorable to after-ripening. While we did not employ other alternating temperatures than those above, we are led to believe that there is always some favorable constant temperature at which after-ripening will take place most readily, and that any variation from this temperature either above or below will retard it.

There is considerable variation in the time in which individual seeds after-ripen, as is indicated in table III and again in those seeds that were removed from the cold too soon. In the latter case there was always a large number of seeds that failed to germinate. These in nearly all cases would germinate if the testas were removed, but when not so treated and left at high temperatures, they would lie upon the moist cotton for weeks without germinating. The higher temperatures seem to inhibit the process of after-ripening. The process of after-ripening then is interesting in that it does not obey the VAN'T HOFF temperature law for rate of chemical reactions, but goes on faster at low temperatures. If this temperature law applies to the individual metabolic processes involved in after-ripening, it must apply to them with quite different coefficients, with the general result that the process as a whole falls with a rise of temperature.

While the results with low oxygen pressure were mainly negative or nearly so in all cases, we are not prepared to say that after-ripening cannot take place under low oxygen pressure or even in the entire absence of oxygen if sufficient time is allowed, but oxygen certainly favors after-ripening. We are now carrying on experiments to determine more definitely the various points in reference to after-ripening and oxygen pressure.

Light does not seem to enter into the after-ripening of the hawthorn to any great extent. At the optimum temperature after-

ripening goes on equally well in dark or light. At a temperature considerably above the optimum, but not sufficiently high to stop the process altogether, light does appear to have some influence, as is indicated in table III.

The seeds of the hawthorn will germinate at a temperature slightly above 0° C. We have found them in nature germinating in early spring, when the ground was yet quite cold and wet. Seeds placed on ice for after-ripening germinate in this condition after going through that process. The germination, however, takes place irregularly, and often requires a considerable period before all the seeds of the culture are germinated. But if the seeds are removed from the cold when they show signs of germinating, and placed at the temperature of the greenhouse, the germination takes place very rapidly, often reaching 90 per cent or more within two or three days. The sudden change of temperature when the after-ripening is complete acts as a powerful stimulus to germination, but if after-ripening is not complete, it seems to inhibit the latter.

How widespread this condition of seeds is, which requires after-ripening, that is, some change involving the embryo itself before germination becomes possible, is not known. All seeds that are slow to germinate, from whatever cause, have too frequently been put into this class. In most cases the delay is evidently not to be found in the embryo at all, but in the seed coat or some other external structure which prevents or limits the taking up of water or oxygen or mechanically inhibits growth. The only way to determine whether the delay is due to after-ripening or to hindrance of incasing structures is to remove the external parts and subject the embryo to germinating conditions.

Dr. ECKERSON of this laboratory is making a study of the internal changes that take place in the seeds of the hawthorn during the process of after-ripening. The work is now well under way.

Conclusions

The seeds of the hawthorn do not germinate immediately after the fruit has ripened, but have a latent period of one or more years.

The cause of the delay is very largely in the hypocotyl rather than in the cotyledons or any of the external structures.

If the seeds are removed from the carpels and kept very moist and at a temperature of 5° or 6° C., the latent period may be shortened to 2.5–3 months, and if the testas are removed and the embryos treated, the period may be reduced to 30 days. Temperatures below 0° C. are not favorable for after-ripening. Seeds kept at −2° to −3° C. did not after-ripen. Seeds at 0° C. after-ripened, but not so readily as those kept at a few degrees above 0° C. The most favorable temperature for after-ripening seems to be 5°–6° C.

Low temperatures alternating with high temperatures are not favorable for after-ripening.

If the seeds are removed from the cold chamber before they have passed through the after-ripening period and subjected to the temperature of the greenhouse, the high temperature either stops or greatly retards the process of after-ripening.

If the seeds are completely after-ripened and removed from the cold to the temperature of the greenhouse, they germinate very quickly. The high temperature greatly stimulates the process of germination.

After-ripening readily takes place under ordinary oxygen pressure, but it has not been fully determined to what extent the oxygen pressure may be reduced and the process still go on.

The pulp, carpels, and seed coat itself tend to delay the process of after-ripening, probably by preventing the free access of water. The changes that take place in the embryo during the after-ripening are not yet known.

Seeds treated dry as well as those treated under water did not after-ripen.

While after-ripening and germination in the hawthorn is a continuous process, that is, we cannot tell where one leaves off and the other begins, the optimum temperature for the latter is considerably above the optimum for the former.

In conclusion, we wish to express our thanks to Dr. WILLIAM CROCKER, at whose suggestion this work was undertaken and who offered many valuable suggestions during its progress.

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THE STRUCTURE OF THE STOMATA OF CERTAIN CRETACEOUS CONIFERS[1]

W. P. THOMPSON

(WITH PLATES V AND VI)

The structure of the stoma is remarkably uniform in all members of the plant kingdom, from *Anthoceros* to the highest angiosperms. It consists essentially of an aperture surrounded by two guard cells which may be more or less sunken and protected by adjacent cells. The only deviation from this organization has been described for the fossil genus *Frenelopsis*, first by ZEILLER,[2] and more recently by BERRY.[3] These authors state that in place of the usual two guard cells, each stoma of *Frenelopsis* is surrounded by four or five guard cells in the form of a rosette. The uniqueness of this supposed condition made it desirable that the subject should be reinvestigated, and for this purpose I have had access to material of *Frenelopsis occidentalis* (Heer), supplied by Professor ZEILLER from a collection made at Nazareth, Portugal, by Professor CHOFFAT.

The characters of the genus *Frenelopsis* have been given in detail by ETTINGSHAUSEN,[4] SCHENK,[5] and others. It is a cretaceous conifer of disputed affinities, being referred by some authors to the Cupressineae and by others to the Gnetales. The leaves are decussately arranged in twos or fours at the nodes of the jointed stem. They are reduced, squamiform, and appressed. The internodes functioned as leaves.

The epidermal characters of *Frenelopsis occidentalis* have been

[1] Contributions from the Phanerogamic Laboratory of Harvard University, No. 45.

[2] ZEILLER, R., Observations sur quelques cuticules fossiles. Ann. Sci. Nat. Bot. **6**:13. 1882.

[3] BERRY, E. W., The epidermal characters of *Frenelopsis ramosissima*. BOT. GAZ. **50**:305–309. *figs 2*. 1910.

[4] ETTINGSHAUSEN, C., Abhand. k.k. geol. Reichsanstalt. Vol. I.

[5] SCHENK, H., Palaeontogr. **19**:13. —.

described by ZEILLER.[6] The cells are rather small, roughly rectangular, and very thick-walled. The very numerous stomata are arranged in irregular lines which give a striated appearance to the unmagnified specimen.

A single stoma is shown in surface view in fig. 1. The central aperture is surrounded by the five "guard" cells of BERRY and ZEILLER. A conical projection can be distinguished extending from each cell to the common center and together forming the rosette. These projections are really below the surface, and, since they are in focus, the opening at the surface is indistinctly seen above them as a pentagonal area whose walls coincide with the bases of the cones.

A clearer idea of the relation of the parts may be obtained from fig. 2, which is a photograph of a vertical section through one of the stomata. The conical processes of the so-called "guard" cells are here seen to project into the middle of a cavity. At the upper limit of this cavity, that is, at the surface, the epidermal cells again approach each other to form, not conical projections, but the pentagonal opening seen indistinctly in the photograph of the surface. These complicated cells are regarded by both BERRY and ZEILLER as guard cells, obviously unlike the guard cells found anywhere else in the plant kingdom. ZEILLER compares them with those of *Marchantia* as follows:

> Le seul fait qui me semble avoir quelque analogie avec cette constitution particulière des stomates, serait celui qu'on observe chez les Marchantiées, où les pores stomatiques sont bordés par cinq ou six cellules, mais qui laissent entre elles une ouverture en forme de canal, et non pas une fente en étoile, comme dans l'espèce dont je viens de parler. Il serait cependant assez singulier et assez peu vraisemblable que cette forme étoilée des stomates fût un fait isolé, n'existant que chez le seul *Frenelopsis Hoheneggeri*, et peut-être faut-il s'attendre à la retrouver quelque jour sur d'autres plantes fossiles, sinon même dans la nature vivante.

In his conception of their arrangement, BERRY disregards that part of the cell above the diverticulum, although he figures it in his low-power drawing.[7] Aside from their unique number and disposi-

[6] ZEILLER, R., Elements de palaeobotanique. Paris. 1900.

[7] *Loc. cit.*, p. 307.

tion, it is difficult to imagine how these structures could effectually serve as guard cells.

The proper conception of the arrangement and homologies of these parts may be most easily obtained from an examination of living forms. The conditions existing in *Agathis bornensis* are represented in fig. 6, which is a photograph of a vertical section of the base of the leaf of that species. The two conspicuous oval cells almost in contact are the sunken guard cells. Inclined above them, with their small extremities at the strongly cutinized surface, are the accessory cells. Each of the latter is seen to have a slight *projection* into the cavity some distance above the guard cells. Viewed from the surface (fig. 7), the accessory cells are seen to be *four* in number surrounding the opening. From the same viewpoint, the guard cells (fig. 8) are seen to be *two* in number, and arranged in the usual manner.

These conditions at once suggest that the so-called guard cells of *Frenelopsis* are really accessory cells, and that we must look below them for the true guard cells. As stated by both BERRY and ZEILLER, structural material of the epidermis only is available, so that the depressed guard cells are not likely to have been preserved. Nevertheless, diligent search reveals their presence in many favorable specimens. Fig. 3, which is a photograph of another stoma in section, shows two well-preserved guard cells at the bottom of the cavity into which the conical structures project. Fig. 4 shows another stoma with unmistakable guard cells below the accessory cells. In this figure the end of a projection from another accessory cell has been cut off and appears in the center of the stomatic cavity. In the majority of the stomata examined in section, no guard cells can be distinguished; in others, fragments have been preserved, especially the outermost wall, which appears to have been more strongly lignified; in still others, the whole structure is preserved in exactly the relations which one would expect in living material.

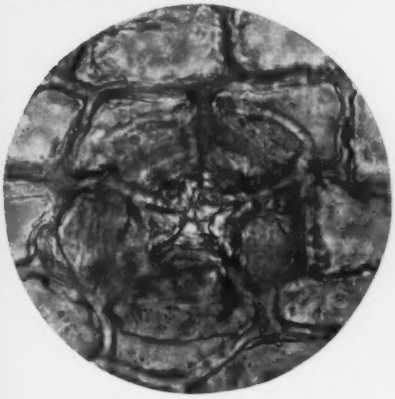
It is still more difficult to observe the guard cells in surface view, owing to the fact that they are covered by the extremely thick accessory cells. This circumstance also entirely precludes their reproduction by photograph. Nevertheless, examination of the

epidermis from beneath reveals their presence in a condition of good preservation in some instances, and of imperfect preservation in many others. A camera lucida drawing showing their typical arrangement above the accessory cells (below in nature) is presented in fig. 5. They are seen to have the normal form. The thinness of their walls probably accounts for the imperfect state of preservation.

That true guard cells of the normal form are present in *Frenelopsis*, in addition to the remarkable accessory cells, is further indicated by the similar conditions presented by other cretaceous plants. A case in point is furnished by *Androvettia statenensis* Hollick and Jeffrey. Fig. 9 is a photograph showing the general features of the epidermis of the species. The cells are very thick-walled and irregular in shape. The numerous stomata lack the definite arrangement characteristic of *Frenelopsis*. The more highly magnified representation given in fig. 10 shows the presence of accessory cells around the stomata as before. In this case they lack the conical projections of *Frenelopsis*, the opening having a uniform outline. The presence of true guard cells is strikingly illustrated in the figure, the aperture appearing as a conspicuous slit across the space surrounded by the accessory cells. Owing to the good condition of preservation of this plant, the guard cells are distinguishable in the majority of cases. Nevertheless, in poorly preserved specimens they have often been destroyed just as in *Frenelopsis*. Fig. 11 shows two stomata from which the guard cells have completely disappeared, although the accessory cells are present in their normal condition.

Another cretaceous fossil possessing both true guard cells and accessory cells is *Brachyphyllum macrocarpum* Newberry. A section parallel to the surface of the leaf of this plant is shown in fig. 12. In each of the stomata the two guard cells are seen to be surrounded by four accessory cells.

The evidence herein adduced from the structure of the stomata of modern conifers, from the conditions presented in fossils of the same geologic age, and above all from actual observations both in section and surface views of *Frenelopsis* itself, appears to show conclusively that true guard cells are present in this genus, and that the



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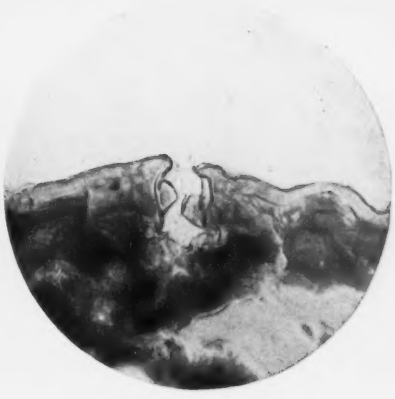

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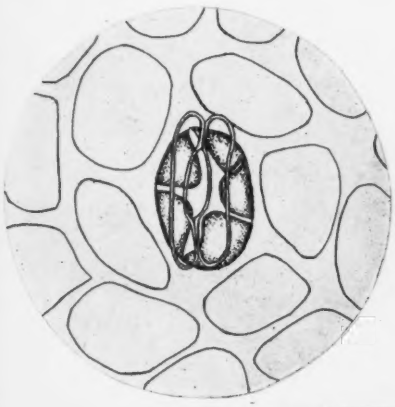

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THOMPSON on STOMATA

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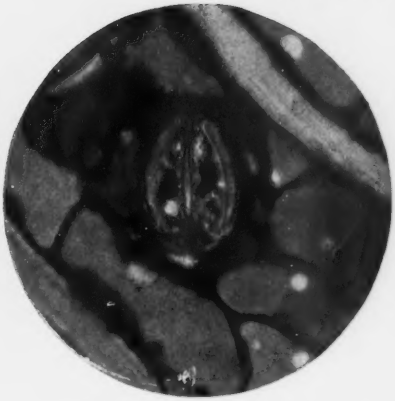

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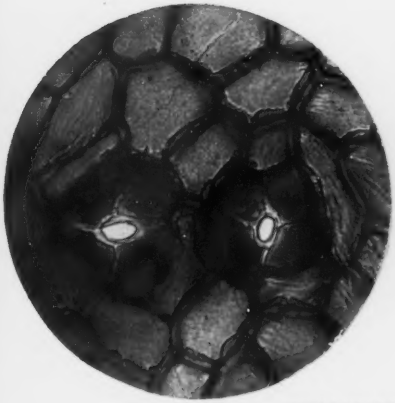

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so-called guard cells are really the commonly occurring accessory cells. The only recorded exception to the remarkably uniform organization of the stoma in the Embryophyta thus disappears.

The writer is indebted to Professor JEFFREY for the material used in this investigation, which was carried on under appointment as an 1851 Exhibition Science Research Scholar of the University of Toronto.

HARVARD UNIVERSITY
CAMBRIDGE, MASS.

EXPLANATION OF PLATES V AND VI

FIG. 1.—*Frenelopsis occidentalis:* stoma in surface view, showing the rosette of projections; ×333.

FIG. 2.—The same: vertical section through a stoma, showing the projections into stomatal cavity; ×250.

FIG. 3.—The same: vertical section of another stoma, showing two guard cells below the accessory cells; ×250.

FIG. 4.—The same: another stoma with distinct guard cells; ×250.

FIG. 5.—The same: camera lucida drawing of stoma from beneath, showing two guard cells above the accessory cells.

FIG. 6.—*Agathis bornensis:* vertical section of base of leaf, showing two guard cells sunken beneath conspicuous accessory cells; ×333.

FIG. 7.—The same: section parallel to the surface, showing stomatal opening surrounded by four accessory cells; ×333.

FIG. 8.—The same: section parallel to the last but deeper—below the accessory cells and including the two guard cells; ×333.

FIG. 9.—*Androvettia statenensis:* surface view of epidermis; ×63.

FIG. 10.—The same: higher magnification, showing two guard cells below accessory cells; ×250.

FIG. 11.—The same: stomata from which the guard cells have disappeared; ×250.

FIG. 12.—*Brachyphyllum macrocarpum:* section parallel to the surface, showing accessory and guard cells; ×125.

BRIEFER ARTICLES

EDUARD STRASBURGER[1]

(BORN FEBRUARY 1, 1844; DIED MAY 19, 1912)

(WITH TWO PORTRAITS)

In the death of STRASBURGER, professor of botany in the University of Bonn, science has lost one of its greatest investigators. His publications, extending over nearly half a century, naturally give the impression that he was a very old man, but such was not the case, for he was only in his sixty-ninth year, and was still actively engaged in research and teaching, when the end came suddenly through an attack of heart disease.

STRASBURGER was a native of Russian Poland, and began his education at Warsaw, studying later at Bonn and at Jena. He traveled extensively in Europe, and in 1873, with HAECKEL, he visited Egypt and the Red Sea, but most of his vacations were spent in Italy, on the Riviera. His wife died several years ago, but his children survive him. He was devoted to his family, was proud of his children, and during the long period while Mrs. STRASBURGER was an invalid, he always found time to accompany her in her daily walk through the beautiful gardens of the old Poppelsdorfer Schloss, once the palace of the Electors of Cologne, but now serving as the botanical laboratory and home of the professor of botany. With others also he was kindly and easy to approach, so that

[1] An account of STRASBURGER'S laboratory and work, written by Professor J. E. HUMPHREY, was published in this journal eighteen years ago (BOT. GAZ. **19**: 401–405, with portrait. 1894).

his students found in him not only a teacher, but also a sympathetic friend, interested in their researches, but also interested in their welfare after leaving his laboratory.

His first publications dealt with the embryology of gymnosperms, then with the more minute details of the life-history of angiosperms. In these researches he showed a profound grasp of the fundamentals of comparative morphology and gradually turned more and more to the study of the cell, until his laboratory became recognized as the most important cytological center in the world.

He was a remarkable lecturer. Although a master artist, he seldom used the chalk, but presented his subject in such vivid word pictures that any further illustration seemed unnecessary. His usual lectures to students covered morphology from the algae to the flowering plants, and every Friday he gave a lecture, open to the public, upon some botanical subject of popular interest.

In the research laboratory he visited every student every day, and always had some helpful suggestion or criticism, but the student would learn on the first day that STRASBURGER had no time to waste. This daily round, in which he might visit as many as eight investigators, seldom occupied more than half an hour, but occasionally, after the usual laboratory hours or on Sundays, he would come into the laboratory, when only one or two students were present, and talk familiarly on various subjects for an hour or more. He seemed particularly attached to his American students. It was my privilege to know him rather intimately at Bonn, and during the ten years which have elapsed since my return, a constant correspondence has continued the inspiration and helpfulness received while at his laboratory. Some quotations from this correspondence will be of more interest than anything else one could write. In a letter of June 29, 1910, he says: "I prize very highly the kindly recogni-

tion of my scientific efforts by my American colleagues. It is a great pleasure to note the tremendous advances of our science in the United States, and to be able to say to myself that in some measure I have been responsible for it."

Of the greatest interest is a letter of October 2, 1908, written in response to a request for some data to be used in an historical seminar at the University of Chicago.

LIEBER HERR KOLLEGE:

You overestimate my contributions! I myself am inclined to believe that I have often failed and only in part attained the scientific ideal which hovered before me. However, in the investigation of life everything is still in flux, the solution of the problems lies in the distant future, and the best that can be said of any one of us is that he was a necessary stage along the way to knowledge. What gratifies me particularly is that in my lecture-room and laboratory I have inspired competent, gifted men of high ideals to strive for the same goal which hovers before me, and that my work shall continue to live in theirs.

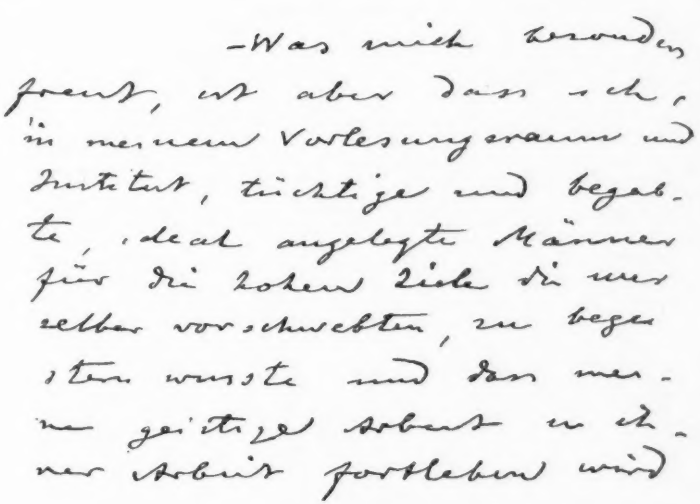
Since you wish to know it, I was born on February 1, 1844. I studied first at Bonn, where I gained technical skill under HERMANN SCHACHT, and at the same time found a great stimulus in the lectures of JULIUS SACHS, who at that time was a teacher in the Poppelsdorf Agricultural Academy. The sudden death of SCHACHT made me decide to go to Jena to PRINGSHEIM, who had met me in his visits to SCHACHT, and who invited me to become his assistant. The critical mind of PRINGSHEIM reacted beneficially upon me, while my association with ERNST HAECKEL soon made me enthusiastic over the great problem presented by CHARLES DARWIN.

My acquaintance with my ten years older teacher soon became friendship, and I have to thank ERNST HAECKEL that two years after my promotion in Jena, when PRINGSHEIM retired, I was called to his place. I was then 25 years old. I was never closely associated with HOFMEISTER. Unfortunately, during the latter part of his life, HOFMEISTER became very sensitive and was angry with me because in 1869 in my work on *Befruchtung bei den Coniferen* I sought to prove that the "corpuscula" do not correspond to the embryo sacs of angiosperms, but are archegonia. HANSTEIN came to Bonn as professor after I had already settled in Jena. In 1887 I came to Bonn as HANSTEIN'S successor. I had been teaching in Jena for twelve years.

With hearty greeting, your very devoted,

E. STRASBURGER

In his correspondence with his colleagues, STRASBURGER never used a typewriter, feeling that a typewritten letter indicated haste and lack of respect. The following is a reproduction, slightly reduced, of a noble paragraph from the above letter.



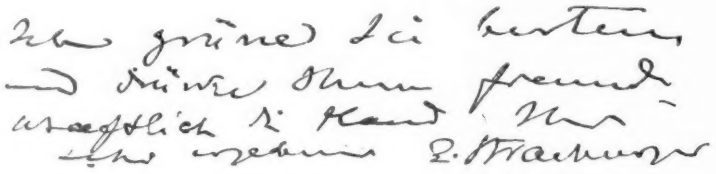
STRASBURGER felt keenly the attack made upon him on account of his paper on graft hybrids. He felt it beneath his dignity to reply, but in a letter of January 6, 1910, he says: "I had the position to defend which I have held in regard to the rôle of the nucleus in fertilization and heredity, and which WINKLER threatened to overthrow. That alone was responsible for my paper in the *Berichte der deutschen botanischen Gesellschaft*."

For some time he had known that his health was failing, but he had continued to work, and his publications show that he was still in his prime and that advancing years had only brought their experience and power without weakening his initiative or enthusiasm in research. At the time of his death, he was deeply interested in the problem of the determination of sex and had investigations under way bearing upon this important subject, but was being delayed by another piece of work. In a letter of March 5, 1911, he writes:

> Unfortunately, I have not got to my microscopic work this winter. A year ago I saw myself necessitated to take part in a scientific publication of pretentious scope, bearing the name *Kultur der Gegenwart*, which is to present in accessible form the whole field of science. The plan may be good in itself, but I have often deplored that I allowed myself to undertake the work and that I must devote to it, rather than to my own research, the few years of scientific activity which still remain for me. Besides, I have not felt well this winter,

and in spite of the advice of my physician, have had to work hard. Day after tomorrow I start for the Riviera and shall see whether I may not recuperate a little.

At the present time a *Festschrift* is under way to commemorate STRASBURGER'S seventieth birthday. A complete account of his life and work will doubtless be published, but a brief notice is appropriate at this time, and the words from his own pen will be appreciated by his numerous pupils and friends. The photograph taken in his regalia, while he was president of the University of Bonn, was given with the injunction that it must not be shown in Germany nor published anywhere during his lifetime. The other photograph was taken in 1892.



—CHARLES J. CHAMBERLAIN, *The University of Chicago*

CURRENT LITERATURE

BOOK REVIEWS

The Chicago textbook[1]

Of the three parts composing the Chicago *Textbook of Botany for Colleges and Universities*, "Morphology" by COULTER and "Physiology" by BARNES appeared nearly two years ago, and were noticed in this journal[2], while "Ecology" by COWLES, concluding the work, appeared in January and is now before us.

However eagerly parts I and II were anticipated by all concerned with botanical education, an even warmer welcome has been ready for part III, because, while the former had predecessors, the latter has not. What, then, are the characteristics of this first compendious textbook of ecology? In the first place, as most botanists will notice with pleased surprise, the book is primarily a description and analysis of the ecological factors, treated in connection with the principal organs—roots, stems, leaves, etc.—with which they are most closely associated; while the synthetic phases of the subject—those discussions of associations, formations, societies, etc., which have to come to stand in the minds of most people as synonymous with the very word ecology—are relegated to a single brief chapter. This is wise, because it is becoming quite plain that the relative barrenness of synthetic ecology is a natural consequence of the newness, crudeness, and deficiencies of our knowledge of analytical ecology. In the second place, the book is a remarkably clear and forceful presentation of its subject, the exposition, indeed, being in no wise inferior to the high standard of the preceding parts, while occasional important passages (e.g., the description of photosynthesis on pp. 525–526) are notably effective. Furthermore, a striking quality of the book is completeness, but it is a question whether in this feature a virtue has not been carried so far as to constitute a fault; for so detailed is the treatment, and so obvious is the intention to leave no important phase of the subject untouched, that the work is carried out of the field of the textbook, in which rigid selection and proportion are essential, into that of the handbook, where completeness is of course a very first requisite. This view receives incidental confirmation from the length of this part in comparison with the others, for it comprises no less than 479 pages, as contrasted with the 296 of part I, which covered all of morphology,

[1] COULTER, BARNES, and COWLES, A textbook of botany. Vol. II. Ecology. 8vo, pp. 480. *figs.* 535. New York: American Book Co., 1912. $2.00.

[2] BOT. GAZ. **51**:67. 1911.

including the whole range of the groups, and the 189 of part II, which comprised all of physiology. So gross a relative disproportion between bulk and intrinsic content value, while unjustifiable from the textbook point of view and prohibitive of the acquisition by a student of any such clear-cut and well proportioned view of its subject as parts I and II afford, is perhaps allowable on the ground of the genuine need for a first formulation of the material. In the third place, the book displays the same wealth of well selected illustration, and the same tasteful, even beautiful typography of the earlier parts. And finally, so far as the accuracy of the fact-matter is concerned, it will require a vastly larger knowledge of the material than the present reviewer possesses to detect any considerable error either of statement or omission, while such flaws as appear are too insignificant for mention. It is, in brief, a distinctive, authoritative, foundational work, destined to take an immediate place as an indispenable reference work for all concerned with the life-phenomena of plants.

A remarkable feature of the book consists in its philosophy. This may be summarized as a systematic antagonism to everything Darwinian. Under the assumption that the language commonly in use to describe the relations of plants to their surroundings, including such words as adaptation, adjustment, storage, etc. (p. 487), mislead learners into a belief that plants act with an even more than human forethoughtfulness (p. 950), the author attempts to avoid all such expressions, visiting with especial condemnation anything of teleological implication. But only a bogey of his own creating is at the bottom of the author's trouble. No students, in the reviewer's experience, if only half-decently instructed, ever gather any such notions. Besides, Darwin himself, as to whose views, of course, there is difference of opinion, but as to whose rationalistic habit of mind there is none, habitually uses teleological language throughout his works without ever having been misunderstood in this respect. However, Professor COWLES is apparently not an evolutionist, because, after expressly and repeatedly combating the idea of a historical or causative adaptation, which he makes either an accident or a psychological illusion, he replaces it by the idea of "mechanical causation" (p. 487), that is, passive reaction to mechanical, physical, or chemical influences. Now this idea carries the inevitable corollary that such responses must be always the same in the same part under the same conditions, and that therefore they cannot be modified into anything else, any more than chemical compounds can change the nature of their reactions to outside influences; and without such possibility of change, no evolution, but only a kind of spontaneous creation, is possible. In his opposition to everything savoring of adaptation, the author is led at times even to a distorted representation of the views he opposes. Thus, no authors, that the reviewer can recall, and certainly none of authoritative rank, have ever maintained any such naïve conception of adaptive response as is attributed to some of them, by implication, at the top of p. 950. Indeed, the author's view of everything relating

to adaptation is distinctly myopic, and the treatment of those subjects tends to the dogmatic, not in language but in spirit. This very book seems to the reviewer to show that whatever the deficiencies of the adaptation-selection hypothesis, it still has to its credit a notable balance of reasonableness in comparison with the proposed substitute.—W. F. GANONG.

An elementary text

A new elementary text by BERGEN and CALDWELL[3] attempts to meet the growing demand for practical botany, which means the economic aspects of plants. This demand arises not only from the interest of pupils in the "bread and butter" side of science, but also from what is thought to be the greatest need of that very large proportion of high-school students whose formal education ends with the high school. There is no question that advantage should be taken of interest and need, and the only question is as to whether they are satisfied by a proposed course of study. Moreover, this question can be answered only by experience. Many a public demand voices a real need, and then the change comes to stay; and many another public demand voices an imaginary need, and then the change soon passes into the limbo of "fads."

The book before us has been handicapped in setting the task of meeting a possible public need and at the same time meeting the artificial need of entrance requirements imposed by colleges. As a result, the unifying motive is lacking and the book becomes a mosaic rather than a definite pattern. The field of previous texts is covered, and to this is added the economic phases of plants, which compels a brevity of treatment in many cases that results in obscurity. In spite of the divergent purposes and space limitations, the book is a marked advance in the direction intended.

Some of the noteworthy features are: an introductory general survey of plants in relation to man, and "the plant as a working unit" (pp. 23); elementary forestry (pp. 21); plant breeding (pp. 21); plant industries (pp. 30); weeds (pp. 11); leading families of flowering plants and their uses (pp. 35); and especial emphasis upon plant diseases and methods of control. In a practical botany of 513 pages, one is surprised to find no less than 214 pages devoted to plant groups. However, economic significance has frequently determined the selection of the forms discussed. With the exception of most of the material treated under "The great groups of plants" (pp. 156–370), the text has a decided flavor of elementary agriculture and might well serve as a text in elementary agricultural botany, though such an important topic as seed testing and selecting is conspicuous by the absence of any special treatment. The numerous footnotes and references to literature should prove both useful and stimulating, at least to instructors. The introduction of

[3] BERGEN, J. Y., and CALDWELL, O. W., Practical botany. pp. v+545. *figs. 381*. Boston: Ginn & Co., 1911.

numerous new and well chosen cuts is refreshing. Unquestionably the book is a valuable addition to elementary texts in botany and should find a wide field of usefulness in the hands of trained instructors.—LEROY H. HARVEY.

MINOR NOTICES

Nature sketches.—The chief scientific value of HANCOCK'S *Nature Sketches*[4] is the large number of accurate and original observations upon insects and other animals in relation to their natural environments. The first chapter contains an unusually clear and simple discussion of problems and theories of evolution. Insect and bird pollination, and the relations of animals to flowers are discussed and beautifully and accurately illustrated, especially in the second chapter, by drawings, photographs, and colored plates of examples from temperate America. The adaptations of insects, birds, and flowers are discussed, and the author appears to be of the opinion that everything is useful. It is unfortunate that the idea of adaptation should be introduced without qualification into a popular work at a time when many botanists and zoologists regard it as doubtful. The chapters on "Animal behavior" and "Ecology" should have had less comprehensive titles. Though somewhat confused with faunistic geography, the first five pages of the chapter on ecology are devoted to a good summary of some of the important facts of genetic ecology. The lists of plant and animal habitats at the end of the book give the habitat preferences of a number of Orthoptera, but contain few elements of progress in ecological classification. The current classification has not been followed.[5] In addition to its scientific value, the book is a good introduction to many aspects of natural history for the lay reader.—V. E. SHELFORD.

Popular manuals.—The nature and purpose of the very interesting *Cambridge manuals of science and literature* have been noticed in this journal.[6] At that time five volumes dealing with plants had been published, and now two additional volumes have appeared: *Links with the past in the plant world*, by A. C. SEWARD (pp. 142); *Life in the sea*, by J. JOHNSTONE (pp. 150). The volumes are sold for one shilling each, and form for the general reader a readable résumé of current scientific knowledge. The titles of the eight chapters of Professor SEWARD'S volume will give a better conception of the contents than does the general title. They are as follows: "Longevity of trees, etc."; "The geographical distribution of plants"; "The geological record"; "Preservation of plants as fossils"; "Ferns, their distribution and antiquity"; "The redwood and mammoth trees of California"; "The Araucaria family";

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[4] HANCOCK, JOSEPH L., Nature sketches in temperate America. 8vo. xviii+451. *pls. 12. figs. 215.* Chicago: A. C. McClurg & Co. 1911. $2.75.

[5] PEARSE, in Science **34**:37. 1912, is mistaken in this matter.

[6] BOT. GAZ. **52**:234. 1911.

"The maiden hair tree." The American publisher is G. P. PUTNAM'S SONS of New York.—J. M. C.

North American Flora.[7]—Vol. VII, part 3, continues the treatment of the Uredinales and contains the Aecidiaceae from *Prospodium* to *Dichaeoma* by JOSEPH CHARLES ARTHUR, the text for the genus *Gymnosporangium* being contributed by FRANK DUNN KERN. One new genus (*Argomyces*) is proposed, which has a geographical distribution from New Mexico and Texas through Mexico and the West Indies to South America, and is represented at present by four known species. Further new species are characterized in the following genera: *Earlea* (1), *Kuehneola* (1), *Spirechina* (1), and *Xenodochus* (1).—J. M. GREENMAN.

NOTES FOR STUDENTS

Variation curves.—Several years ago papers dealing with variation in the number of parts of flowers, flower heads, inflorescences, etc., were of frequent appearance. As the novelty of the method disappeared, the number of contributors to the knowledge of such variations has decreased, but, as is usually true in such cases, the value of the contributions has correspondingly improved. Several recent studies in this field are of exceptional interest.

VOGLER[8] gives a large number of counts of ray flowers in *Chrysanthemum*, *Boltonia*, and *Senecio*. In *Chrysanthemum Parthenium* he found a curve having the mode on 21 when the plants were grown on well-manured soil, and on 13 when grown on infertile soil, the curves being strongly skew in each case toward an intermediate point, the mean values lying between 14 and 19. These results agree essentially, therefore, with those of KLEBS[9] on *Sedum spectabile*. In *Boltonia latisquama* the ray flowers have a wide range of variation (39–81), with the summit of the curve near 55. Three different plants were separately counted in three successive years, and although the different seasons differed considerably, there was no corresponding change in the number of ray flowers. One of these plants had each year the mean number approximately 57, another approximately 54. These permanent differences are probably not to be attributed to genotypic differences in the plants, however, as they originated from a common stock by vegetative division. In *Senecio alpinus* a count of over 3000 heads from two different localities in three different years gave in every case a nearly monomodal curve with the mode on 19, thus convincing the author of the limitations of Ludwig's law that the maxima of such

[7] North American flora. Vol. VII, part 3, pp. 161–268. The New York Botanical Garden. April 15, 1912.

[8] VOGLER, P., Variation der Anzahl der Strahlblüten bei einigen Kompositen. Beih. Bot. Centralbl. **25**: 387–396. 1910.

[9] KLEBS, G., Studien über Variation. Arch. Entwick.-Mech. Organ. **24**: 29–113. 1907.

variation curves fall upon the numbers of the Fibonacci series, 2, 3, 5, 8, 13, etc., and low multiples of them, or on the similarly constituted "Trientalis-series," 3, 4, 7, 11, etc., and their low multiples. The latter series was discovered by LUDWIG in *Trientalis*, whence its name. VOGLER[10] had found earlier that the modes in the number of umbellary rays of *Astrantia major* fall upon members of the Fibonacci series when only the primary umbels are included, but in the secondary umbels the modes are on the Trientalis series. More recently the same author[11] has reported on the number of ray flowers in *Arnica montana*, *Buphthalmum salicifolium*, *Eupatorium molle*, *Aster novi-belgii*, *Senecio erucifolius*, and *Chrysanthemum Parthenium*. Several of these species gave well-marked modes on the Fibonacci numbers, but in other collections of data from the same species the mode occurred not infrequently on some quite unrelated number. For example, in *Arnica montana* a collection from Rigi, Switzerland, in 1908, showed modes on 13, 16, and 21, while heads of the same species collected the next year at Klosters presented a well-developed mode on 11 and only a slight indication of a mode on 13. Later analysis of this case showed that the terminal heads give modes on 13 and 16, while secondary heads give modes on 11 and 14, the latter numbers bearing the same relation to the Trientalis series that the former do to the Fibonacci series. This whole problem as to the position of the modes in variation curves of ray flowers, and other organs which are related more or less definitely to the phyllotactic spiral, is still unsolved, though it is evident that the Fibonacci series supplies the modal numbers in many cases, and that other equally definite series are followed in other cases. It is very rare that the number of variates used by investigators is sufficiently great to establish with any considerable degree of probable correctness these relatively superficial features of the curves. RITTER has gone to the length of asserting that non-phyllotactic variates among plant organs have their modal numbers also related to the Fibonacci or Trientalis series. He even contends that this is true of graduated variates. In support of this view he tabulates[12] a rather meager series of measurements of width and length of leaves and leaflets of *Stellaria media*, *Oxalis Acetosella*, *Lysimachia nummularia*, *Hypericum perforatum*, *Caragana arborescens*, *Rosa canina*, *Medicago sativa*, *Symphoricarpus racemosus*, *Fragaria vesca*, and *Cytisus Laburnum*, and the width and length of fruits of *Alnus glandulosa*, *Rosa canina*, *Quercus Robur*, and *Q. sessiliflora*. He believes that the measurements of surfaces, such as leaf blades, give modes related to the square roots of the Fibonacci numbers, namely, on $10\sqrt{1}$, $10\sqrt{2}$, $10\sqrt{3}$, $10\sqrt{5}$, $10\sqrt{8}$, etc.,

[10] VOGLER, P., Variationstatistische Untersuchungen an den Dolden von *Astrantia major*. Beih. Bot. Centralbl. **24**: 1–9. *figs. 6*. 1908.

[11] VOGLER, P., Neue variationstatistische Untersuchungen an Compositen. Jahrb. St. Gallischen Naturwis. Gesells. 1910: 1–32. 1911.

[12] RITTER, G., Über discontinuirliche Variation im Organismenreiche. Beih. Bot. Centralbl. **25**: 1–29. 1909.

and that in tri-dimensional material such as fruits, the modes are related in similar manner to the cube roots of the Fibonacci numbers. The absurdity of such a view will be obvious when it is considered that nature takes no note of such arbitrary units of measure as the millimeter and centimeter, and that the choice of any other unit of measure would place the modes on other values. VOGLER[13] shows by a much more extensive series of measurements of leaflets of *Cytisus Laburnum* that while the curves are multimodal, the modes can not by any sort of manipulation be made to fit the Fibonacci series.

In another paper, VOGLER[14] performs an important service by summarizing the statistical studies which have been made upon the heads of Compositae and the umbel rays of the Umbelliferae, together with a few of the more important investigations upon the flowers and inflorescences of other species. The list of Compositae includes 45 species and of the Umbelliferae 10 species. The list gives not only the names of the species and the particular organs studied, but also states the number of counts upon which conclusions regarding the several species have been based, the apparent modes, and references to papers in the appended bibliography in which the results are recorded. This bibliography contains 63 titles.

DE BRUYKER[15] makes an extensive study of variation in the umbels of *Primula* the motive for presenting a discussion of the entire subject of statistical variation. This simple and concise presentation of the subject should occupy for Dutch readers a place similar to that held by JOHANNSEN'S[16] discussion for readers of German. It is not necessary here to consider the general treatment of the subject of variation as given by DE BRUYKER, but only the new results relating to *Primula officinalis*, *P. farinosa*, and *P. elatior*. The modal numbers of flowers in the inflorescences of these three species fall with considerable regularity upon the numbers of the Fibonacci series, but collections taken at different parts of the season show a gradual decrease in the average number of flowers per inflorescence as the season progresses. Plants growing in a favorable environment had the mode on 5, and in less favorable ones on 3. The similarity of results in collections from good and bad surroundings, and in early and later parts of the season, convinces the author of the correctness of the interpretation of the gradual fall in mean number of parts during the

[13] VOGLER, P., Die Variation der Blattspreite bei *Cytisus Laburnum* L. Beih. Bot. Centralbl. **27**: 391–437. *figs. 12*. 1911.

[14] VOLGER, P., Probleme und Resultate variationstatistischer Untersuchungen an Blüten und Blütenständen. Jahrb. St. Gallischen Naturwis. Gesells. 1910: 33–71. 1911.

[15] DE BRUYKER, C., De statistische methode in de plantkunde en hare toepassingen op de studie van den invloed der levensvoorwarden. pp. 226. *figs. 33*. Gent: A. Siffer. 1910.

[16] JOHANNSEN. W., Elemente der exakten Erblichkeitslehre. pp. vi+516. *figs. 31*. Jena: Gustav Fischer. 1909.

season, which attributes it to a change of nutrition, an interpretation which was given independently by MACLEOD and the reviewer about ten years ago. The polymorphism shown by the multimodal curves is interpreted by DE BRUYKER as due to differences in nutrition acting in conjunction with a discontinuous mode of development, through which the new organs tend to be added in groups instead of singly. The same explanation or one essentially similar is applicable to other multimodal variation curves, the series of modes being determined by the manner in which each succeeding group of organs added is related to the preceding group or groups.

DE BRUYKER recognizes nine series of modes for multimodal variation curves. These are as follows: (*a*) the powers of 2 (2, 4, 8, 16, etc.), as in the peristome teeth of mosses; (*b*) multiples of 3 (3, 6, 9, 12, etc.), as number of flowers in *Lonicera caprifolium;* (*c*) multiples of 4 (4, 8, 12, 16, etc.), as in the number of flowers per umbel in *Cornus Mas;* (*d*) multiples of 5 (5, 10, 15, 20, etc.), as in the number of stamens in *Pyrus communis;* (*e*) the Fibonacci-Ludwig series (1, 2, 3, 5, 8, [10], 13, [16], etc.), as in many Compositae, Umbelliferae, etc.; (*f*) the Trientalis series (1, 3, 4, 7, 11, 18, etc.), as in *Trientalis*, secondary umbels of *Astrantia major*, lateral heads of *Arnica*, etc.; (*g*) Cardamine series (2, 5, 8, 11, 13, 16, 19, 22), as found by VOGLER for the number of flowers in *Cardamine pratensis;* (*h*) the odd series (1, 3, 5, 7, 9, etc.), as in number of leaflets in imparipinnate leaves, etc.; (*i*) the even series (2, 4, 6, 8, etc.), as in paripinnate leaves, rows of grains on ears of maize, etc.

By selecting for higher number of rays in *Calliopsis bicolor*, under conditions of high nourishment, DE BRUYKER was able to secure a strain of this species, by far the largest number of whose heads had 13 rays, though the material with which he began selecting gave a very high percentage with only 8 rays. This result corresponds with that of DEVRIES with *Chrysanthemum segetum*. The sensitive period for the influence of nourishment on the number of ray flowers was investigated in *Chrysanthemum carinatum*, and this period was observed to close four or five weeks before the opening of the heads. DE BRUYKER'S work closes with a succinct statement of the principal results of the author's investigations on *Primula elatior*, *Chrysanthemum carinatum*, *C. segetum*, *Calliopsis bicolor*, *Scabiosa atropurpurea percapita*, rye, barley, and wheat. The bibliography contains references to a few more than 100 papers dealing with the subject of variation and its statistical study, and a full index is added.

NIEUWENHUIS[17] has studied the changes in the variations and in the mean values of the number of ray flowers in nine species of Compositae from the beginning to the end of the flowering season. He finds in seven of these species an essential agreement with the behavior found by the reviewer[18] in *Aster*

[17] NIEUWENHUIS, M., Die Periodicität in der Ausbildung der Strahlblüten bei den Kompositen. Recueil Trav. Bot. Néerl. **8**: 108–181. *figs. 23.* 1911.

[18] SHULL, G. H., Place-constants for *Aster prenanthoides*. BOT. GAZ. **38**: 333–375. 1904.

prenanthoides. The characteristic periodicity curve of mean values in these species rises quickly to a maximum in the early part of the season, after which there is a much more gradual decline until the end of the season. Only in *Melampodium divaricatum* and in *Cosmos sulfureus* was there no essential change throughout the season, the former species having a single mode on 10 with the mean slightly above 10 in every collection made, and the latter species presenting a similar constancy, having at all times a half-curve, falling steeply from a strong mode on 5 only to higher values. In most of these species the modes were on the Fibonacci numbers; and while the changes in mean values were gradual and continuous, the appearance of modes on intermediate numbers was relatively rare. In *Anthemis Cotula* 11 and 9 appeared as transition modes between 13 and 8; 9 also appeared momentarily in *Zinnia Haageana*, *Z. tenuiflora*, and *Laya platyglossa;* and 11 and 12 in *Sanvitalia procumbens*. In three heterocarpous species, *Dimorphotheca pluvialis*, *Laya platyglossa*, and *Sanvitalia procumbens*, the plants grown from the two kinds of seeds produced essentially like variation curves. The same thing was true of plants grown in different years and in different environments, the modal numbers and characteristic slopes of the periodicity curves remaining unchanged for the particular species, though the mean values were considerably modified.—GEO. H. SHULL.

Roots of Psaronius.—Since the removal of the great mass of the marattiaceous plants of the Paleozoic to the seed plants, more critical attention has been given to *Psaronius* as the sole evidence of the existence of the Marattiaceae at that early period. Among the structures differentiating *Psaronius* from modern Marattiaceae, the most striking is the difference in the location of the secondary roots in relation to the stem. In the modern representatives of the family these roots bore their way for a considerable distance through the cortex of the stem before they penetrate to the surface. At all points in their course they are sharply marked off from the cortex by remnants of broken-down cells. In *Psaronius* they form a wide zone in the cortex of the stem in which there are no remnants of leaf traces or leaf scars, and no sharp distinction between the root cortex and the parenchyma in the interstices between the roots. STENZEL's explanation of this root layer as homologous with the outer cortex of the Marattiaceae has passed current without question until the last ten years. In 1902 FARMER and HILL suggested that the parenchyma in the interstices of the roots of *Psaronius* might be of the nature of hairy outgrowths rather than cortical parenchyma of the stem.

The question thus raised has been attacked by SOLMS-LAUBACH[19] with convincing results. He worked cheifly with thin sections of fossils (*P. Haidingeri*) from Manebach, supplemented by material from the Museum of Rio

[19] SOLMS-LAUBACH, H. GRAFEN ZU, Der tiefschwarze *Psaronius Haidingeri* von Manebach in Thüringen. Zeitschr. Bot. 3:721–757. *figs* 7. 1911.

Janeiro. He finds that, unlike the modern Marattiaceae, *Psaronius* has a thin cortex bounded on the outside by a massive hypodermal sclerenchyma layer. From the outer region of this sclerenchyma layer or from the epidermis strands of tissue develop by a secondary activity of the cells, giving rise to a clothing of multicellular hairs on the surface of the stem. Where the secondary roots make their way through the cortex and sclerenchyma layer, they are limited, as in modern Marattiaceae, by a definite epidermis and by a zone of disintegrated cortical cells. But after they have penetrated the sclerenchyma layer, no such clearly marked boundary is perceptible, for here the roots pass downward among the multicellular hairs on the outside of the stem. They are consequently imbedded in the hairs which form a filling tissue between them, closely applied to the stemward sides of the roots. Then, in turn, the hypodermal layer of the cortex of the roots starts into activity. The resulting cells are few on the inner surface of the roots, where the hairs from the stem are in contact with them, while on the outwardly turned face they develop outgrowths similar to the multicellular hairs of the stem. These in turn make an imbedding layer for younger roots whose origin is higher in the stem, and which grow downward over the root surfaces as the first roots grew over the stem. While the hairs of the stem fill the crevices between the first roots and are soon overgrown by them, similar outgrowths from the roots fill the spaces between the successive layers of roots. Each system of hairs stops its growth in so short a time that a meristematic part of the tissue can never be detected. No branching of the filling tissues appears, because of the constant correspondence between the increase in the circumference of the stem and the number of cell rows in the filling tissue, due to the increase in the number of points of origin.

If it were possible to follow a root throughout its course, it would be found to be organized in three parts: a proximal part, in which it breaks its way through the cortex of the stem; a middle part, applied to the filling tissue arising from the stem; and a distal part, in which the subepidermal cortical tissue develops. The so-called "inner" and "outer" roots of *Psaronius* illustrate the two last mentioned portions.

In an attempt to find whether this peculiar development of the outer cortex is present in plants related to *Psaronius*, SOLMS-LAUBACH examined a stem of *Xylopsaronius*. Though its poor state of preservation made definite conclusions impossible, the presence of the root of another plant between the sclerenchyma layer of the stem and the inner roots is strong evidence of a resemblance. In confirmation of this, SCHÜSTER[20] has shown complete correspondence between a well-preserved root system of *Xylopsaronius* and *Psaronius*. The tissue formerly interpreted as secondary xylem in the root of *Xylopsaronius* is in reality secondary filling tissue originating from the cortex like that described in *Psaronius* by SOLMS-LAUBACH. His photomicrograph of

[20] SCHÜSTER, J., *Xylopsaronius*, der erste Farn mit secundärem Holz? Ber. Deutsch. Bot. Gesells. **29**:545–548. 1911.

the stem is strong evidence in support of the interpretation of the filling tissue as peculiar outgrowths. Nothing comparable to such multicellular hairs on roots has been found in present ferns, although it is possible that examination of tropical tree ferns may reveal traces of similar structures.—GRACE M. CHARLES.

The development of Pyronema confluens.—Believing that the alternation of generations has not yet been satisfactorily worked out in any fungus, CLAUSSEN[21] has completed an extensive cytological and morphological study of the development of *Pyronema confluens*, a form already investigated by HARPER[22]. The spores germinate immediately on being discharged from the ascus. He finds that under favorable conditions any cell of the fungus may develop into a complete plant. In material grown on agar at 20° C. in direct sunlight, he finds that the vegetative mycelium is produced in 1–2 days; the fruit bodies begin to form in 2–3 days; fertilization occurs in 3–4 days and the first ascogenous hyphae appear; after 5 days the recurved tips of the ascogenous hyphae are observable; young asci may be found on the sixth day, at which time 1, 2, 4, and 8-spored asci are present. In cultures under these conditions the fungus completes its development in 7–8 days. CLAUSSEN observed that the younger stages of the fruit bodies often arise from dichotomously branched aerial hyphae, so that they are often stalked. His observations as to the origin of the sexual organs agree in general with the earlier descriptions of DE BARY[23] and of KIHLMAN.[24] The hyphae, which bear the ascogones, and those which bear the antheridia, may arise from the same mycelial thread; the fungus, therefore, is homothallic.

The mycelium consists of multinucleate cells. Protoplasmic streaming was observed in the hyphae, indicating that there is a pore in the cross-walls, connecting the contents of adjacent cells. The hyphal branches which bear the sexual organs are always multinucleate. CLAUSSEN is unable to determine whether or not nuclear division occurs in the ascogone and in the antheridium before fertilization. So far as he is able to discover, the nuclei in the sexual organs are exactly alike. When the sex organs are mature, he observes that the nuclei increase in size, but that there is a more marked increase in the size of the nuclei of the ascogone. Certain nuclei in both male and female organs degenerate before the sexual act. The phenomena concerned in the fusion of the antheridium with the trichogyne, the passage of the male nuclei into the

[21] CLAUSSEN, P., Zur Entwicklungsgeschichte der Ascomyceten. *Pyronema confluens*. Zeitschr. Bot. **4**: 1–64. *pls. 6. figs. 13.* 1912.

[22] HARPER, R. A., Sexual reproduction in *Pyronema confluens* and the morphology of the ascocarp. Ann. Botany **14**: 321–400. 1905.

[23] DE BARY, A., Ueber die Fruchtentwicklung der Ascomyceten. Leipzig. 1863.

[24] KIHLMAN, O., Zur Entwicklungsgeschichte der Ascomyceten. Acta Soc. Scient. Fenn. **13**: 29–40. 1883.

trichogyne and thence into the ascogone, is essentially as has been described by HARPER and others. After the sexual act is completed and the trichogyne is again cut off from the ascogone, many nuclei were observed in the ascogone in pairs. On account of the slight difference in size of the paired nuclei and of the nucleoli, he believes each pair consists of a male and female nucleus. A fusion of these paired nuclei does not occur in the ascogone, but they enter the ascogonous hyphae in pairs. BROWN[25] holds that there is no fusion of the sexual nuclei in the ascogonium. He holds that an appearance quite like fusion results from division of the nuclei, the daughter nuclei remaining closely associated.

The ascogenous hyphae were observed to develop in several different ways. Whatever the method of their development, CLAUSSEN believes that the sexual nuclei and their progeny formed by conjugate division remain entirely distinct. A pair of each of the nuclei finally enters the young ascus, where they fuse to form the primary ascus nucleus. CLAUSSEN finds it difficult to make out the structure of the fusion nucleus of the ascus. He is convinced that the first division of this nucleus is heterotypic, and finds a synaptic contraction and a diakinesis, in which there are about 12 bivalent chromosomes. At no point in nuclear division has he been able to distinguish central bodies with certainty. In the second and third divisions of the ascus nuclei he fails to find a synaptic contraction or a diakinesis stage. The number of chromosomes in these divisions is about twelve. The process of spore formation and spore delimitation is essentially as described by HARPER.

According to CLAUSSEN, the spore, mycelium, and sexual organs constitute the gametophyte, while the ascogenous hyphae represent a sporophyte not sharply separated from the gametophyte. The ascus is a spore mother cell. The sporophyte, instead of having nuclei with double chromosome numbers, contains male and female nuclei in pairs, which divide by conjugate division. The nuclear divisions in the ascus, except the first, have no significance in the alternation of generations in this fungus.—J. B. OVERTON.

Cytology of Laboulbeniales.—In a short introductory account based on the results of his studies of the cytology of a number of forms of the Laboulbeniales, FAUL[26] gives the general outlines of the morphology of this group. The spores in the earliest stages of their formation are uninucleate, but before the spore is mature the nucleus divides and a septum is formed, dividing the spore into two cells. In *Amorphomyces* alone the septum is not formed and the nucleus degenerates. The cells of the thallus are characteristically uninucleate, but after the thallus has completed its growth some of the

[25] BROWN, W. H., Nuclear phenomena in *Pyronema confluens*. Johns Hopkins Univ. Circ. **6**:42–45. 1909.

[26] FAUL, J. H., The cytology of the Laboulbeniales. Ann. Botany **25**:649–654. 1911.

larger cells become multinucleate. The nuclear divisions are mitotic throughout. The antheridia in all cases are uninucleate. In the forms with exogenous antheridia the uninucleate spermatia arise as branchlike outgrowths from the antheridia. It is probable that the antheridial nucleus divides repeatedly to furnish nuclei for the successively formed spermatia. In the forms with endogenous antheridia, the antheridial nucleus divides and the sperm nucleus is pushed out by the spindle fibers toward the opening of the antheridium through which the spermatia are discharged. The spermatia consist of the relatively large nucleus, apparently surrounded by only a little cytoplasm, and the protoplasmic membrane. The antheridial nucleus divides repeatedly to form successive sperm nuclei which are ejected by the spindle fibers in the peculiar manner described.

The origin of the binucleate state of the carpogenic cell was made out only in *Laboulbenia chaetophora*, which has no antheridia. In the other forms neither the entrance of the sperm nucleus into the trichogyne nor its migration through the trichophoric cell has been observed. In *Laboulbenia chaetophora* the nuclei of the trichophoric and the carpogenic cells divide, and one nucleus from each pair ultimately constitutes a member of the pair in the carpogenic cell. From the carpogenic cell the ascogonium and ascogenous cells are formed after a series of conjugate nuclear divisions. Asci bud off directly from the binucleate ascogenous cells. The subsequent processes of nuclear fusion in the ascus and spore formation differ in no essential detail from the analogous processes among the Ascomycetes with which the Laboulbeniales are usually classed.

The conclusion drawn by the author from the cytological study of the Laboulbeniales is that they belong to the Ascomycetes, and more particularly, on account of the possession of a perithecium, to the Pyrenomycetes. The phenomena occurring in the ascus appear to lend some support to this classification, but the author's attempt to homologize the perithecium of the Laboulbeniales with that of the Pyrenomycetes would seem to need further support. Thus far the unique development of the perithecium of the Laboulbeniales has no known analogies among the Ascomycetes.—H. HASSELBRING.

Sexuality in mosses.—MARCHAL,[27] in a study of sexuality in mosses, makes a comparison of a dioicous species, *Bryum caespiticium*, with a number of synoicous species, chief among which is *Amblystegium serpens*. In the dioicous species one-half of the spores give rise to protonemata which produce antheridial plants, the other half produce archegonial plants. Fertilization produces a bisexual sporophyte and the sex characters are separated in the reduction division. Consequently two members of the tetrad are always male and two female, as has actually been shown in *Sphaerocarpus*. In synoicous forms the

[27] MARCHAL, EL., La sexualité chez les Mousses. Bull. Soc. Roy. Belgique **47**: 277–285. 1911.

gametophores from protonemata produced by spores, as well as those from secondary protonemata rising from the stem, leaves, and even from the wall cells of antheridia and archegonia, are always bisexual, and the sex characters are not separated until the last division of the spermatogenous and the oogenous cells. The sex characters are united by fertilization and not separated in the tetrad. Therefore in dioicous mosses the sex characters are separate in the spores, protonemata, gametophores, sperms, and eggs, but not in the sporophyte; in synoicous mosses the sex characters are separate only in the egg and sperm.

MARCHAL is able to induce apospory in the capsule of *Bryum caespiticium*. Gametophores rising from an aposporous protonema are *always synoicous*, but the eggs are never fertilized. He concludes that dioicous mosses which have become synoicous through apospory are irremediably sterile. In the synoicous *Amblystegium serpens* apospory was also induced, and the resulting gametophores produced eggs capable of being fertilized. In the $4x$ sporophytes from these fertilized eggs, apospory was again induced, but the $4x$ leafy shoots, although exceptionally vigorous, have as yet remained persistently sterile. The same results were obtained in other synoicous species, *Amblystegium subtile*, *Barbula muralis*, and many others which the author does not name. He states that *Ephemerum serratum* and *Funaria hygrometrica* are synoicous. Miss SPEER, working in the Hull Botanical Laboratory, first showed that the latter species is occasionally synoicous. MARCHAL is at present studying a sterile synoicous *Bryum atropurpureum* which he believes is a natural aposporous derivative of the common dioicous form.

There are no illustrations, and no definite information as to how the presence of $2x$ and $4x$ numbers in the aposporous derivatives were proved; nor are the methods for inducing apospory and for continuing the cultures given in detail. It is an admirable piece of much-needed research, but the lack of a definite and detailed statement of methods is a very unfortunate omission, since many investigators look with suspicion on the work of those who are secretive as to methods when fundamental problems are concerned.—W. J. G. LAND.

Phytomyxaceae.—SCHWARTZ, who has recently made several contributions to our knowledge of the parasitic slime molds, gives an account[28] of another form which he found on the roots of *Poa annua* and other grasses. The organism, to which he gives the name *Sorosphaera graminis* without, however, adding a formal diagnosis, is closely related to *S. Junci*, which the author discovered in the roots of sedges. The organism was found most abundant on plants whose roots were hypertrophied by eelworms. It is not usually found, however, in the swollen parts, nor does the organism itself produce any form of hypertrophy. The life-history of *S. graminis* does not

[28] SCHWARTZ, E. J., The life-history and cytology of *Sorophaera graminis*. Ann. Botany **25**:792–797. 1911.

differ from that of *S. Junci*, but some of the stages appear to be more easily observable in *S. graminis*. The youngest stages are uninucleate amebae. These fuse to form plasmodia which grow until they occupy the entire host cell. The nuclei of the growing plasmodia all divide repeatedly and simultaneously in the manner described for other members of the Plasmodiophoraceae. At the close of the vegetative stage the akaryote or chromidial stage begins. The nuclei lose their contents, leaving only vacuoles in their place. Within these vacuoles apparently fresh nuclei are organized. These undergo mitotic divisions, after which the plasmodium is broken up by cleavage into small uninucleate masses which become the spores. Under the classification of MAIRE and TISON, this form would be placed in their genus *Ligniera*, which includes those species of the Plasmodiophoraceae which lack the schizogenous stage and do not cause swelling on their host plants.—H. HASSELBRING.

Zygopteris.—SCOTT[29] has studied sections of a new specimen of *Zygopteris Grayi*, and finds that it is an *Ankyropteris*, as BERTRAND had pointed out, on the basis of the presence of peripheral loops on the leaf trace. The vascular cylinder of the stem (a 5-rayed star in section) is regarded as "a highly elaborated protostele," there being at present no evidence for the existence of a true pith in any member of the group. This is certainly a simpler interpretation of the pithlike region with interspersed tracheids than to regard the cylinder as a "condensed" polystelic structure. It would be even simpler to eliminate "highly elaborated," and to call the cylinder an incomplete protostele. The problematical and abundant "aphlebiae" are found to be "modified basal pinnae of the leaf, as shown by the structure and mode of origin of their vascular strand."—J. M. C.

Effect of temperature on respiration.—KUIJPER,[30] while at the Buitenzorg laboratories, determined the CO_2 production by seedlings of *Arachis hypogaea* and *Oryza sativa* at various temperatures from 15° C. to 50° C. He finds that the effect of temperature on respiration of the tropical plants studied is the same as on plants in the temperate zone.[31] But the "critical temperature" (temperature at which a high respiratory intensity is maintained for a considerable time) of *Arachis hypogaea* is 5°–10° higher than that previously found for *Pisum* and *Lupinus*. KUIJPER thinks this difference is due to their surroundings. The mean temperature at Java is about 10° higher than the mean temperature of the vegetation period of the temperate zone.—SOPHIA H. ECKERSON.

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[29] SCOTT, D. H., On a paleozoic fern, the *Zygopteris Grayi* of Williamson. Ann. Botany **26**: 39–69. *pls. 1–5. fig. 1.* 1912.

[30] KUIJPER, J., Einige weiteren Versuche über den Einfluss der Temperatur auf die Atmung der höheren Pflanzen. Ann. Jard. Bot. Buitenzorg II. **9**: 45–54. *pls. 6, 7.* 1911.

[31] BOT. GAZ. **50**: 233. 1910.

Doubling of embryo sac.—COMPTON[32] reports an interesting situation in a *Lychnis* hybrid, in which an ovule contained two embryo sacs, each penetrated by a pollen tube, and each containing a two-celled embryo. He calls this "a curious example of duplicity." The closing statement is worth remembering: "The fact that two pollen tubes should enter and fertilize an ovule which had developed two embryo sacs can hardly be a mere coincidence; rather it would seem to indicate a quantitative relation between embryo sac and pollen tube in the matter of chemotaxis, two embryo sacs excreting sufficient of the chemotropic substance to attract two pollen tubes."—J. M. C.

Seedling structure of Centrospermae.—HILL and DEFRAINE[33] have recorded the results of an extended survey of the transition phenomena of the seedlings of Centrospermae. The "theoretical considerations" are to be presented later, but in the present paper there are indications of what they may be. The families presented, through abundant representatives, are Portulacaceae, Caryophyllaceae, Amarantaceae, Chenopodiaceae, Phytolaccaceae, Aizoaceae, and Nyctaginaceae. The authors state that "no very striking results" were obtained, and that the chief interest is connected with the features of the last-named family.—J. M. C.

Fall of leaves.—Based upon a mass of data collected largely from the literature, COMBES[34] shows that the conception of SACHS regarding the migration of substances at the time of leaf fall is no longer tenable. The substances that do not disappear from the leaves, as well as those that accumulate in them before their fall in the autumn, are not to be considered a priori as substances non-utilizable or toxic for the plant containing them. The fallen leaves contain an important percentage of substances that would have been utilizable by the plant.—CHAS. O. APPLEMAN.

Morphology of Viola.—Miss BLISS[35] has studied five species of *Viola* with reference to the structures connected with the embryo sac. The hypodermal archesporial cell, the tapetal cell, the linear tetrad, and all the antefertilization structures of the sac are what may be regarded as normal for angiosperms. Double fertilization was observed in *V. cucullata*. "There is no suggestion of a suspensor," and the embryo, surrounded by a solid mass of endosperm, is bright green.—J. M. C.

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[32] COMPTON, R. H., Note on a case of doubling of embryo sac, pollen tube, and embryo. Ann. Botany **26**: 243, 244. 1912.

[33] HILL, T. G., and DEFRAINE, ETHEL. On the seedling structure of certain Centrospermae. Ann. Botany **26**: 175–199. *figs. 15*. 1912.

[34] COMBES, RAOUT, Les opinions actuelles sur les phenomènes physiologiques qui accompagnent la chute des feuilles. Rev. Gén. Bot. **23**: 129–264. 1911.

[35] BLISS, MARY C., A contribution to the life history of *Viola*. Ann. Botany **26**: 155–163. *pls. 17–19*. 1912.

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